Collembola in a plant diversity gradient: Interactions between the aboveground and belowground system

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Für meine Familie.

Für mich.

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Ehrenwörtliche Erklärung

Ich erkläre hiermit ehrenwörtlich, dass ich die vorliegende Arbeit entsprechend den Regeln guter wissenschaftlicher Praxis selbstständig und ohne unzulässige Hilfe Dritter angefertigt habe. Sämtliche aus fremden Quellen direkt oder indirekt übernommenen Gedanken sowie sämtliche von Anderen direkt oder indirekt übernommenen Daten, Techniken und Materialien sind als solche kenntlich gemacht. Die Arbeit wurde bisher bei keiner anderen Hochschule zu Prüfungszwecken eingereicht.

Darmstadt, den 18.01.2012

_____

Alexander Sabais

„Ich habe keine besondere Begabung, sondern bin nur leidenschaftlich neugierig.“

Albert Einstein 1879-1955

„Gehe nicht, wohin der Weg führen mag, sondern dorthin,
wo kein Weg ist und hinterlasse eine Spur.“

Jean Paul 1763-1825

Curriculum vitae

Alexander Christian Wolf Sabais

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Sabais ACW, Scheu S, and Eisenhauer N (2011) Plant species richness drives the density of Collembola in temperate grassland. Acta Oecologica 37: 195-202.

CHAPTER 3

Eisenhauer N, Sabais ACW, and Scheu S (2011) Collembola species composition and diversity effects on ecosystem functioning vary with plant functional group. Soil Biology and Biochemistry 43: 1697-1704.

CHAPTER 4

Sabais ACW, Eisenhauer N, König S, Renker C, Buscot F, and Scheu S (2012) Soil organisms shape the competition between grassland plant species. Oecologia: submitted.

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Overview of manuscripts

The present thesis comprises the following manuscripts:

Chapter 2 Plant species richness drives the density of Collembola in temperate grassland

by Alexander Sabais, Nico Eisenhauer, and Stefan Scheu. Published 2011 in Acta Oecologica 37, 195-202.

This manuscript investigates how the diversity and composition of the Collembola community are influenced by plant species richness, plant functional group richness and plant functional identity, and if these effects vary with season. It shows that Collembola are significantly affected by plant species and plant functional group richness, highlighting the importance of the singular hypothesis for the belowground decomposer system. Furthermore, effects of the plant community on Collembola indeed vary with season. The results of this manuscript also indicate a distinct time-lag of the response of Collembola to vegetation manipulations.

Alexander Sabais is the overall author of this manuscript. He developed the main ideas and experimental setup. He personally collected and analyzed the data, created the tables and graphs, and wrote the manuscript.

Nico Eisenhauer took over the corresponding authorship, communicated with referees, editors and typesetters, and accomplished the whole publication process from submission to print publication in 2011. He was involved in the development of the experimental setup, analyzed the data, helped sampling and extracting Collembola, and commented intensively on earlier versions of this manuscript.

Stefan Scheu was the supervisor of the experiment presented in this manuscript. He designed the experiment, was involved in the development of the experimental setup, and critically reviewed earlier versions of the present manuscript.

Chapter 3 Influence of Collembola diversity on plant productivity varies with plant functional group identity

by Nico Eisenhauer, Alexander Sabais, and Stefan Scheu. Published 2011 in Soil Biology and Biochemistry 43, 1697-1704.

This manuscript investigates effects of Collembola diversity on plant growth and decomposition processes. It shows that both plant productivity and litter decomposition are significantly affected by Collembola diversity and that effects of Collembola diversity on plant productivity and decomposition processes depend on plant functional group identity. Furthermore, the results suggest that competitive interactions among Collembola species modify effects of Collembola on plant productivity and decomposition.

Nico Eisenhauer is the overall author of this manuscript. He was involved in the development of the experimental setup and helped maintaining and harvesting the greenhouse experiment. He helped analyzing data and commented on earlier versions of this manuscript. He finalized the manuscript, communicated with referees, editors and typesetters, and accomplished the whole publication process from submission to print publication in 2011.

Alexander Sabais developed the main ideas and experimental setup. He personally collected and analyzed the data, created the tables and graphs and wrote the earlier versions of this manuscript.

Stefan Scheu was the supervisor of the experiment presented in this manuscript. He was involved in the development of the experimental setup and critically reviewed earlier versions of the present manuscript.

CHAPTER 4 SOIL ORGANISMS SHAPE THE COMPETITION BETWEEN GRASSLAND PLANT SPECIES

by Alexander Sabais, Nico Eisenhauer, Stephan König, Carsten Renker, Francois Buscot, and Stefan Scheu. Submitted to Oecologia.

This manuscript investigates the interactive effects of Collembola and mycorrhizal fungi on the performance and the competition between plant species from three functional groups (grasses, herbs and legumes). It shows that Collembola and mycorrhiza interactively impact belowground competition by selectively affecting the productivity of certain plant species and that mycorrhiza mediate effects of Collembola on plant productivity and nutrient acquisition.

Alexander Sabais is the overall author of this manuscript. He developed the main ideas and experimental setup. He personally collected and analyzed the data, created the tables and graphs, wrote the whole manuscript.

Nico Eisenhauer was involved in the development of the experimental setup and helped maintaining and harvesting the greenhouse experiment. He helped analyzing data and commented on earlier versions of this manuscript. He took over the corresponding authorship and communicated with referees and editors.

Stephan König was involved in the development and setup of the experiment. He provided data on the mycorrhization of plant roots and commented on previous versions of this manuscript.

Carsten Renker was involved in the development of the experimental setup and commented on previous versions of this manuscript.

Francois Buscot was involved in the development of the experimental setup and commented on previous versions of this manuscript.

Stefan Scheu was the supervisor of the experiment presented in this manuscript. He was involved in the development of the experimental setup and critically reviewed earlier versions of the present manuscript.

SUMMARY

During the past few decades, there has been growing understanding that human well-being is fundamentally linked to the state of the environment. The rapid decline of global biodiversity and its consequences for ecosystem functioning therefore has become a focal point of scientific interest and prompted a multitude of biodiversity studies aiming to investigate the complex relationship between plant species richness and ecosystem functioning in terrestrial grassland ecosystems. However, the majority of these studies predominantly focused on the aboveground aspects of terrestrial ecosystems such as plant productivity, neglecting the role of the belowground decomposer community as an important driver of fundamental ecosystem processes. Soil microorganisms and decomposer animals control decomposition processes and nutrient mineralization in soil, processes that are key determinants for plant performance and ecosystem functioning. Collembola are among the most important microarthropods in terrestrial ecosystems as they are known to affect ecosystem processes and plant nutrition by a variety of direct and indirect mechanisms.

The present thesis was conducted within the framework of the Jena Experiment, a large biodiversity experiment aiming to investigate the impacts of declining plant diversity on ecosystem processes and trophic interactions in grassland ecosystems. The overall objective of my thesis was to investigate the effects of plant species richness, plant functional group richness and particular plant functional groups on Collembola communities in temperate grassland and to explore the main mechanisms by which Collembola in turn affect plant communities. These questions were addressed in a field study and two greenhouse experiments.

The intentions of the field study were to assess the effects of plant species richness, plant functional group richness and plant functional identity on the structure of Collembola communities in temperate grassland and if plant community effects on Collembola vary with season. Collembola density and diversity significantly increased with plant species and plant functional group richness, highlighting the importance of the singular hypothesis for soil invertebrates. Generally, grasses and legumes beneficially affected Collembola density and diversity, whereas effects of small herbs usually were detrimental. These impacts were largely consistent in spring and autumn. The results indicate a distinct time-lag of the response of Collembola to vegetation manipulations, suggesting that effects of plant functional group

identity on the belowground system are more immediate whereas effects of plant species and plant functional group richness will become important in the long-term.

The first greenhouse experiment investigated how plant productivity and decomposition processes are influenced by Collembola diversity and if effects of Collembola vary with plant functional group identity. Collembola decreased soil surface litter decomposition whereas root litter decomposition was enhanced. Furthermore, Collembola diversity changed root depth distribution in a plant functional group specific way, indicating distinct changes in plant competition due to changes in Collembola diversity and composition. However, effects of Collembola on plant performance appeared to be idiosyncratic and point to strong context-dependent interactions among Collembola species, such as facilitation or competition for nutrients and living space. The results therefore suggest that changes in Collembola diversity may have unpredictable consequences for ecosystem functioning.

The aim of the second greenhouse experiment was to investigate effects of Collembola and arbuscular-mycorrhizal fungi (AMF) on plant competition and the performance of *Lolium perenne*, *Plantago lanceolata* and *Trifolium pratense* representing three dominant plant functional groups (grasses, herbs and legumes). Further, we investigated variations in Collembola performance and AMF colonization rates of plant roots as influenced by the different plant communities. Collembola did not affect total colonization of roots by AMF but increased the number of mycorrhizal vesicles in *P. lanceolata*. AMF and Collembola both enhanced the amount of N and P in plant shoot tissue, but impacts of Collembola were less pronounced in the presence of AMF. Overall, the results suggest that AMF and Collembola interact in affecting plant competition. Presence of AMF modulated plant specific effects on Collembola and increased the competitiveness of *P. lanceolata* and *T. pratense* against *L. perenne*, pointing to a loose inter-kingdom mutualistic relationship between plant, mycorrhiza and Collembola. The results demonstrate that Collembola and AMF interactively impact the competition between plant species by differentially but concordantly affecting nutrient acquisition of the plant.

The insights of the present thesis corroborate the importance of the belowground community for ecosystem functioning and human well-being by highlighting the interactions within the different levels of soil biota.

ZUSAMMENFASSUNG

Während der letzten Jahrzehnte hat die Einsicht zugenommen, dass das Wohlergehen der Menschheit grundlegend vom Zustand der Umwelt abhängt. Der rasante globale Biodiversitätsverlust sowie die sich daraus ergebenden Konsequenzen für Ökosystemprozesse sind daher in den Fokus der Wissenschaft gerückt und haben zu einer Vielzahl von Biodiversitätsexperimenten geführt, um die komplexen Zusammenhänge zwischen Pflanzenartenreichtum und Ökosystemprozessen in terrestrischen Graslandgesellschaften zu untersuchen. Die Mehrzahl dieser Studien konzentrierte sich allerdings nur auf bestimmte Aspekte terrestrischer Ökosysteme, wie zum Beispiel Pflanzenproduktivität, und vernachlässigte dabei die fundamentale Rolle des unterirdischen Zersetzersystems für die Steuerung von Ökosystemprozessen. Mikroorganismen und Bodentiere steuern Zersetzungsprozesse und Nährstoffkreisläufe, welche als Schlüsselprozesse für die Produktivität und das Funktionieren von Ökosystemen angesehen werden. Collembolen gehören zu den wichtigsten Mikroarthropoden in terrestrischen Ökosystemen, da sie Ökosystemprozesse und die Nährstoffversorgung von Pflanzen durch eine Vielzahl direkter und indirekter Wechselwirkungen beeinflussen können.

Die vorliegende Arbeit wurde im Rahmen des Jena Experiments erstellt, einem großen Biodiversitätsexperiment, in dem die Auswirkungen abnehmender Pflanzendiversität auf Ökosystemprozesse und trophische Interaktionen in einem Graslandökosystem untersucht werden. Die übergeordnete Zielsetzung meiner Arbeit war die Untersuchung der Auswirkungen abnehmender Pflanzendiversität und Anzahl bzw. Identität bestimmter funktioneller Pflanzengruppen auf Collembolengemeinschaften in gemäßigten Graslandsystemen. Zudem sollten die wesentlichen Mechanismen erforscht werden, durch welche Collembolen Pflanzengesellschaften beeinflussen. Um diese Fragestellungen zu beantworten, wurden im Rahmen meiner Promotion ein Feldversuch und zwei Gewächshausexperimente durchgeführt.

Das Ziel des Feldversuchs war es, die Einflüsse von Pflanzenartenzahl, Anzahl funktioneller Pflanzengruppen und der Identität bestimmter funktioneller Pflanzengruppen auf Collembolengemeinschaften zu untersuchen, und herauszufinden, ob es saisonale Variationen im Einfluss der Pflanzengesellschaft auf die Collembolen gibt. Sowohl Dichte als auch Diversität der Collembolengemeinschaft stiegen mit zunehmendem Pflanzenartenreichtum und Anzahl funktioneller Pflanzengruppen an, was auf die Wichtigkeit der „Singular-

Hypothese“ für Bodeninvertebraten hindeutet. Grundsätzlich übten Gräser und Leguminosen einen positiven Einfluss auf Collembolen aus, während die Anwesenheit von kleinen Kräutern in der Regel nachteilig war. Darüber hinaus waren diese Einflüsse im Frühjahr und im Herbst überwiegend einheitlich. Die Ergebnisse weisen zudem auf eine ausgeprägte zeitliche Verzögerung der Collembolenreaktion auf Vegetationsmanipulationen hin, was vermuten lässt, dass Effekte bestimmter funktioneller Pflanzengruppen vergleichsweise unmittelbar erfolgen, während die Einflüsse von Pflanzenartenreichtum und Anzahl funktioneller Pflanzengruppen mehr Zeit brauchen, um sichtbare Auswirkungen zu zeigen.

Im ersten Gewächshausexperiment wurde untersucht, auf welche Weise Pflanzenwachstum und Zersetzungsprozesse durch Collembolendiversität beeinflusst werden und ob sich Effekte von Collembolen auf Pflanzen verschiedener funktioneller Gruppen unterscheiden. Es stellte sich heraus, dass die Zersetzung von Oberflächenstreu in Anwesenheit von Collembolen reduziert wurde, während die Zersetzung von Wurzelstreu beschleunigt wurde. Zudem änderte die Anwesenheit von Collembolen die Durchwurzelungstiefe der Pflanzen in Abhängigkeit ihrer funktionellen Identität, was auf eine ausgeprägte Veränderung der Konkurrenzverhältnisse zwischen Pflanzen aufgrund von Veränderungen in Diversität und Zusammensetzung der Collembolengemeinschaft hindeutet. Die teilweise idiosynkratischen Effekte von Collembolen auf das Wachstum der Pflanzen deuten allerdings auf ausgeprägte, kontextabhängige Wechselwirkungen zwischen den einzelnen Arten hin, wie Förderung oder Konkurrenzkampf um Nahrung oder Lebensraum. Die Ergebnisse dieses Gewächshausexperiments zeigen, dass Veränderungen in der Diversität von Collembolengemeinschaften unvorhersehbare Auswirkungen auf Ökosystemprozesse haben können.

Das Ziel des zweiten Gewächshausexperiments war es, die Einflüsse von Collembolen und arbuskulären Mykorrhizapilzen auf das Wachstum und die Konkurrenzbeziehungen von *Lolium perenne*, *Plantago lanceolata* und *Trifolium pratense* zu erkunden, welche drei dominante funktionelle Pflanzengruppen des Jena Experiments (Gräser, Kräuter und Leguminosen) repräsentieren. Des Weiteren wurde untersucht, inwieweit sich die verschiedenen Pflanzengesellschaften auf das Wachstum der Collembolen und die Mykorrhizierungsrate der Pflanzenwurzeln auswirken. Die Anwesenheit von Collembolen hatte zwar keine Auswirkungen auf die Mykorrhizierungsrate der Pflanzenwurzeln, erhöhte aber die Anzahl der Vesikel in *P. lanceolata*. Sowohl Mykorrhiza als auch Collembolen erhöhten die Stickstoff- und Phosphatmengen im Pflanzensprossgewebe; in Anwesenheit von

Mykorrhiza waren die Effekte von Collembolen allerdings weniger stark ausgeprägt, als ohne die Pilze. Es konnte gezeigt werden, dass sich Mykorrhizapilze und Collembolen in ihrer Wirkung auf Konkurrenzbeziehungen zwischen Pflanzen wechselseitig beeinflussen. Mykorrhizapilze modulierten pflanzenspezifische Einflüsse auf Collembolen und erhöhten die Konkurrenzkraft von *P. lanceolata* und *T. pratense* gegenüber *L. perenne*, was auf eine mutualistische Beziehung zwischen Pflanzen, Mykorrhiza und Collembolen hindeutet. Die gewonnenen Ergebnisse verdeutlichen, dass Collembolen und Mykorrhizapilze in der Lage sind, durch ihr Zusammenwirken pflanzliche Konkurrenzbeziehungen zu verändern, indem sie die Nährstoffaufnahme der Pflanzen auf verschiedene aber gleichgerichtete Weise beeinflussen.

Durch das Hervorheben komplexer Wechselwirkungen untermauern die Erkenntnisse der vorliegenden Arbeit die Wichtigkeit des unterirdischen Zersetzersystems für den Ablauf essenzieller Ökosystemprozesse.

Chapter 1

General Introduction

1.1 BIODIVERSITY AND ECOSYSTEM PROCESSES

Every life form leaves footprint on our planet. And although the human species is neither the largest nor the most common being on earth its footprint easily outmatches all other marks by far. The rapid population growth and the industrial revolution at the turn of the last century led to dramatic changes in land use and to increased levels of atmospheric carbon dioxide due to emissions from fossil fuel combustion and animal agriculture (IPCC report 2007). In conjunction with other **human influences** such as deforestation, over-exploitation, nitrogen deposition, and aerosol and ozone depletion, the evident **climate change** is one of the main drivers of the present dramatic **decline of global species diversity**, rivaling even the magnitude of the five known mass extinctions in Earth's 4.5 billion year long history (Naeem et al. 1999; Table 1.1; Fig. 1.1). In fact, species extinction rates increased about a thousandfold since the appearance of the human race (Vitousek et al. 1997) and it is expected that, even at the lowest estimated extinction rate, about half of our planet's known plant and animal species will disappear within the next 100 years due to human mediated impacts (Soulé 1991, Chapin et al. 2001). Yet, unlike the phases of mass extinction which resulted from natural disasters affecting the worlds ecosystems on a global scale, todays loss of biodiversity can predominantly be ascribed to **anthropogenic factors** (Sala et al. 2000).

Table 1.1 List of the five mass extinctions that occurred during the last 600 million years (adapted from Hallam and Wignall 1997, Sepkosi Jr. and Raup 1986; http://www.deathreference.com/En-Gh/Extinction.html).

	Ordovician-Silurian	Devonian-Carboniferous	Permian-Triassic	Triassic-Jurassic	Cretaceous-Tertiary
When occurred	439 million years ago	365 million years ago	251 million years ago	199-214 million years ago	65 million years ago
Groups affected	Up to 85% of all species and 45-60% of all marine genera	70-80% of all species and 30% of all families	85-90% of all marine and land vertebrate species and 95% of all marine species	More than 75% of all species and 25% of all families	47% of marine genera and 18% of land vertebrates
Hypothesized causes	Unusually fast movement of tectonic plates; glaciation leading to sharp declines in sea levels	Either one catastrophic event or several smaller ones; glaciation and temperature declines; oceanic anoxia	Possible asteroid impact; volcanic eruptions; declines in sea levels and oceanic anoxia	Suspected decline in sea levels and oceanic anoxia; possible asteroid impact	Potential asteroid impact coinciding with Siberian volcanic eruptions and dramatic climate cooling

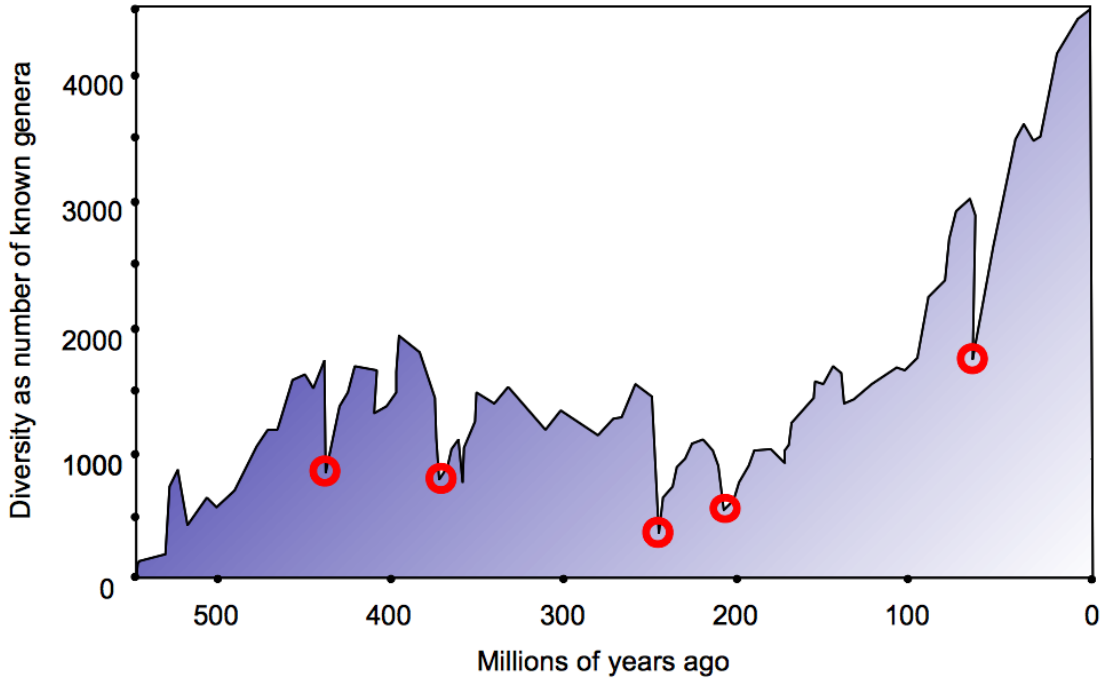

Figure 1.1 The major changes in the diversity of animals and plants from the beginning of the Cambrian period to the present. Note that the obvious increase in recent diversity is likely due to the fragmentary fossil record of many genera. The red circles indicate the five mass extinctions listed in Table 1.1 (modified after Zimmer 2001).

Consequently, it is not surprising that the worldwide decline of species numbers and genetic and functional diversity has raised concern about the effect of biodiversity on ecosystem functioning and human well-being (Schulze and Mooney 1994, Kinzig et al. 2002, Loreau et al. 2002, Fargione and Tilman 2005, Cardinale et al. 2011).

The earth's living organisms contribute to human well-being in a variety of ways. Besides providing goods and products essential to life, such as food, medicine and natural pest control systems, they also mediate local and regional flows of energy and materials, including the recycling of carbon, nitrogen, phosphorous and other elements. These biologically mediated energy and material flows contribute to various **ecosystem services** that ultimately benefit human well-being such as plant growth, erosion control and the regulation of carbon dioxide (Naeem et al. 1999). Scientists therefore argued about the shape of the biodiversity-ecosystem functioning relationship and proposed more than 50 different hypotheses to describe the **consequences of declining biodiversity**. Despite their multitude, most assumptions can be assigned to one of the three general categories of biodiversity functioning hypotheses (Naeem et al 2002, Cardinale et al. 2011; Fig. 1.2):

1. **Redundancy hypotheses**

   These hypotheses imply that initial losses of diversity will result in minimal changes in ecosystem functioning because at least a certain proportion of species are redundant in the processes they perform and their loss is compensated for by other species. However, if the species richness drops below a certain threshold the ecosystem will collapse. The most prominent example of these type of hypotheses is the **rivet redundancy hypothesis** proposed by Ehrlich and Ehrlich (1981), which compares the species number to the rivets on an airplane wing (Fig. 1.2A). By assuming that a wing contains many redundant rivets, a certain number of them can fail until the integrity of the wing finally collapses.

2. **Singular hypotheses**

   Contrary to the redundancy hypotheses, the singular hypotheses imply that each species contributes to ecosystem functioning in a unique way, resulting in detectable changes in ecosystem functioning as the species is lost or added to the community. The loss of ecosystem functioning can either decline linearly with loss of diversity (**proportional loss hypotheses**; Fig. 1.2B) or exponentially, where even minimal species loss results in significant declines in the functioning of ecosystems (**immediate catastrophe hypotheses**; Fig. 1.2C). The latter form of hypotheses often refers to singular species as '**keystone species**' and I will address their role for ecosystem functioning in more detail later in this Chapter (q.v. **Section 1.5**).

3. **Context-dependent or idiosyncratic hypotheses**

   Context-dependent or idiosyncratic hypotheses imply that the impact caused by either loss or addition of species depends on the environmental conditions under which the local extinction or addition occurs, e.g. microclimatic condition, nutrient availability, community composition, or disturbance regime.

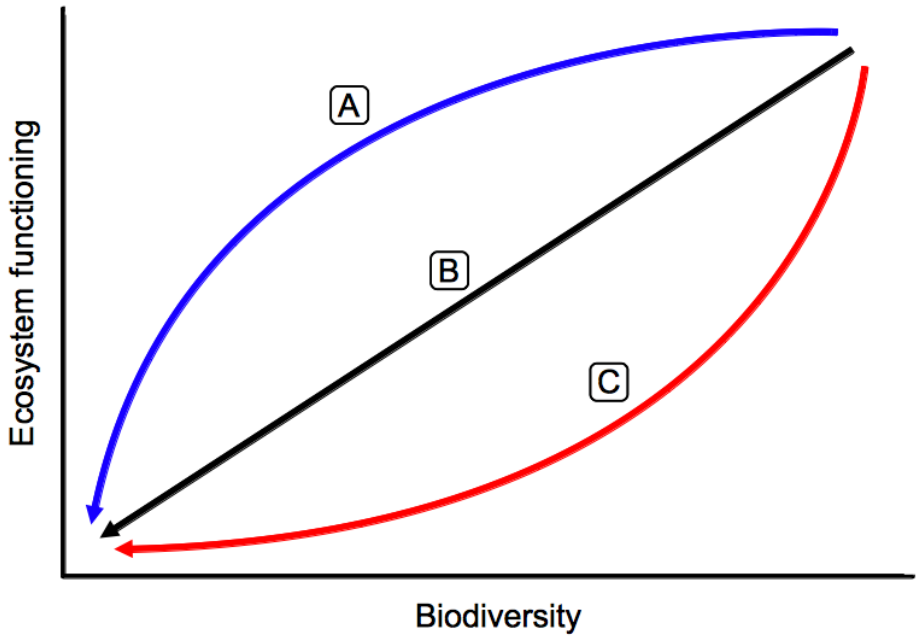

Figure 1.2 General Biodiversity-ecosystem-functioning relationships. (**A**) Rivet Redundancy Hypothesis: initial loss of biodiversity affects ecosystem functioning only little until a certain threshold is reached and the system collapses. (**B**) Proportional Loss Hypothesis: Loss of biodiversity results in linear decline of ecosystem functioning. (**C**) Immediate Catastrophe Hypothesis: Even minimal loss of biodiversity results in significant declines of ecosystem functioning (modified after Cardinale et al. 2011).

The interpretation of results gained from biodiversity experiments is difficult and ultimately requires the consideration of two underlying **mechanisms of species richness effects**, called the "**sampling effect**" and the "**complementarity effect**". The sampling effect can be understood as an indirect diversity effect of community composition rather than species richness *per se*, as it refers to the increased probability of a highly productive or competitive species to be present at high diversity levels (Huston 1997). In contrast, complementarity of species is considered to be the result of niche partitioning, differences in resource requirements or competitive abilities, and **facilitation**, by which certain species modify environmental conditions in a way that promotes the performance of other co-occurring species. In case of complementarity, a more diverse plant community should be able to use available resources more completely, resulting in increased performance of the community when compared to the sum of the expected performances of the individual species growing alone (Loreau 2000, Loreau and Hector 2001). In terrestrial ecosystems, diversity effects appear to be driven equally by selection and complementarity (Cardinale et al. 2011).

Yet, both mechanisms covary and positive complementarity effects may be weakened or even nullified by negative selection effects and *vice versa* (Jiang et al. 2008).

But what exactly is **biodiversity**? The current textbook definition of biodiversity is "variation of live at all levels of biological organization" (Gaston and Spicer 2004). Hence, it does not only encompass the variability among living organisms of all terrestrial and aquatic ecosystems but also includes diversity within species, between species and of ecosystems. Although the term "biodiversity" refers collectively to all these aspects of biotic diversity, the present thesis focuses on biodiversity in terms of **species richness** and **number of functional groups**, where species richness is defined as the number of different species in a given area. The term functional groups on the other hand refers to groups of species that perform similar roles in ecosystems or that share certain traits such as growth form, life history, nutritional needs, physiology or trophic status within a food web. Depending on the ecosystem processes to be studied, scientists may assign a species to one of several different functional groups.

Determining whether biodiversity *per se* is important to the functioning of ecosystem processes is a difficult task since many of the factors that reduce local biodiversity such as habitat conversion also directly affect many ecological processes, thereby masking the more subtle indirect effects of plant species loss (Naeem et al. 1999). However, recent studies indicate that ecosystems are indeed sensitive to changes in the numbers and kinds of species in their communities (Schulze and Mooney 1994, Kinzig et al. 2002, Loreau et al. 2002, Cardinale et al. 2011). They have identified the following **impacts on ecosystem functioning** that often result from loss of biodiversity:

1. Decline of primary production
2. Decreased ecosystem resistance and resilience to environmental perturbations and disturbances such as drought or flooding
3. Increased variability and fluctuation of ecosystem processes such as plant productivity, pest and disease cycles, and soil nitrogen levels

Nevertheless, the lack of knowledge on the role of biodiversity for the functioning of ecosystems has prompted research on the **key components of biodiversity** and its underlying mechanisms and interrelationships. During the past decade, there has been increasing research

studies and experimentation aiming to shed light on the functional consequences of biodiversity loss for ecosystem processes (Naeem et al. 1999, Cardinale et al. 2011).

1.2 BIODIVERSITY EXPERIMENTS

Since Darwin scientists have hypothesized about the relationship between biodiversity and ecosystem functioning, though only the recent worldwide loss of biodiversity has stimulated an unprecedented amount of theoretical, observational and experimental studies.

To assess effects of biodiversity on ecosystem functioning, **two different approaches** can be used. Scientists can either study naturally existing biodiversity gradients to determine relationships between species richness and ecosystem processes, or directly manipulate specific parameters of diversity in specified experiments. The second approach allows for explicit testing of effects of e.g., plant species richness or specific plant functional groups on plant productivity or soil fauna. However, both approaches should not be regarded as separate alternatives as they complement one another to generate a more holistic view of biodiversity effects on ecosystem processes.

The **design of biodiversity experiments** is usually based on a previously defined species pool from which various species combinations are assembled. The majority of experimental studies investigating the relationship between plant species diversity and ecosystem functioning have been conducted in **grassland ecosystems** (Tilman et al. 1996, Spehn at al. 2000, Cardinale et al. 2011). For good reason; except for the Antarctic, grasslands are present on all continents of earth. They are particularly widespread in temperate zones of North America, Russia and Africa (Fig. 1.3). However, the majority of central European grasslands are due to human mediated changes in agriculture and farming practices (Küster 1999). Depending on the intensity of management practices, grassland species richness ranges from very low in highly productive monocultures to very high in extensively used meadows. However, the persistent usage and transformation of grasslands for agriculture fundamentally impacted grassland biodiversity with species richness markedly declining during the last decades (Minns et al. 2001).

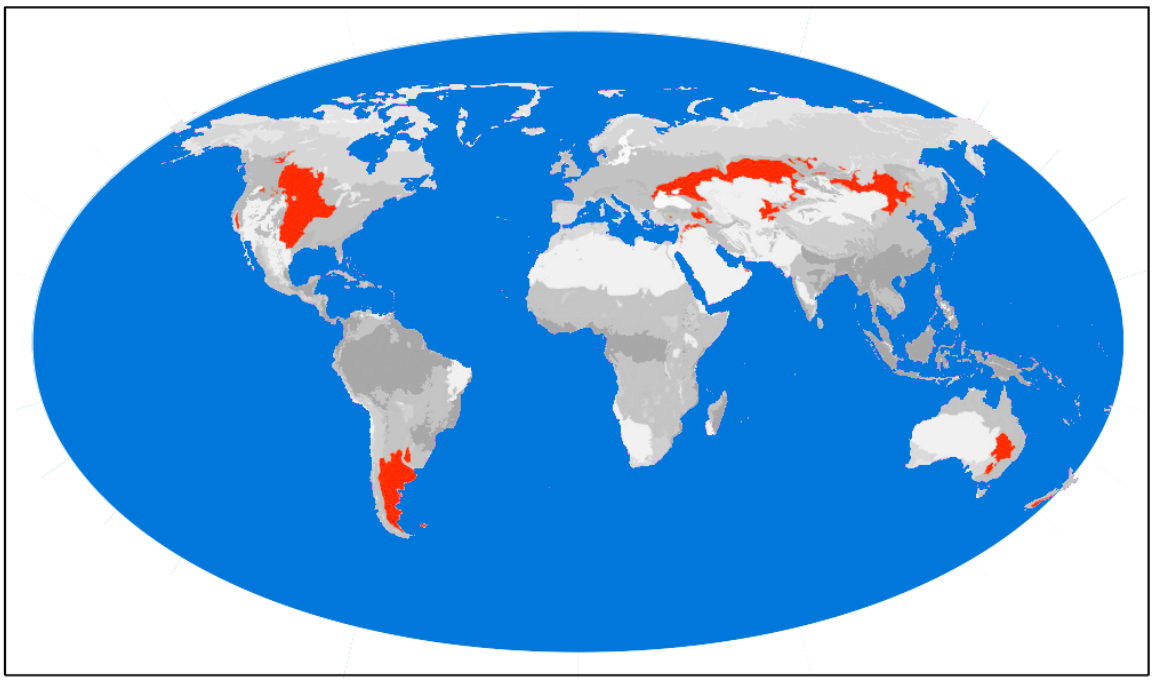

Figure 1.3 Map indicating the worldwide occurrence of temperate grasslands in red (modified after Millennium Ecosystem Assessment 2005; http://maps.grida.no/go/graphic/the-main-biomes-of-the-world).

1.3 THE JENA EXPERIMENT

A major drawback of previous biodiversity experiments is their small scale limiting the value of their results for the general understanding of plant species richness effects on ecosystem processes (Mooney 2002). This problem has been addressed in the design of the Jena Experiment, a large biodiversity field experiment investigating the role of biodiversity for element cycling and trophic interactions in grassland communities (Roscher et al. 2004). In contrast to previous studies, a comparatively large experimental plot size of 20 x 20 m was chosen to allow the establishment of specific nested sub-plots within the respective plant community on which various manipulations could be performed without impeding the overall establishment and dynamics of the plant community (Fig. 1.5F). The present thesis was conducted within "**Subproject 5 – Soil Fauna**" of the Jena Experiment, aiming to investigate the impacts of declining plant diversity on target soil animal groups (Collembola, Lumbricidae and Nematoda) and their interacting effects on ecosystem processes.

The **field site of the Jena Experiment** is located on the floodplain of the Saale river at the northern edge of the city of Jena (Thuringia, Germany; 50°55´N, 11°35´E; Fig. 1.4) at an altitude of 130 m NN. Mean annual air temperature at a meteorological station 3 km south of the field site is 9.3°C (1961-1990) and mean annual precipitation amounts to 587 mm (Kluge and Müller-Westermeier 2000). As typical for a lowland river floodplain, the soil is an Eutric Fluvisol (FAO-Unesco, 1997) developed from up to 2 m-thick loamy fluvial sediments almost free of stones (Roscher et al. 2004). The site was used as grassland in the early 1960ies (Hundt 1961) and highly fertilized over the last decades to establish an arable field for growing vegetables and wheat. The field was harvested last in autumn 2000, ploughed and kept fallow throughout the next year. In order to suppress the establishment of weeds the field was harrowed in June, August and October, and treated with Glyphosate (N-(Phosphonomethyl)-glycine, Roundup) in July 2001 (Roscher et al. 2004). Prior to the establishment of the experimental plots in May 2002, the field site was again harrowed twice within five weeks. The experiment was established on plots of 20 x 20 m which were grouped into four blocks parallel to the Saale river to account for changing soil characteristics with increasing distance from the river, mainly stone surface cover (0-23%), sand content (45-628 g kg^{-1}), and $CaCO_3$ concentration (40-391 g kg^{-1}; Fig. 1.5C; J. Baade, pers. Comm..). Soil variations in pH (7.1-8.4) and total nitrogen concentration (1.0-2.7 g N kg^{-1}) are smaller (CV <21%). As each block contains an equal number of plots, plant species, and plant functional group richness levels, effects of soil heterogeneity can be separated from biodiversity effects in the statistical analysis.

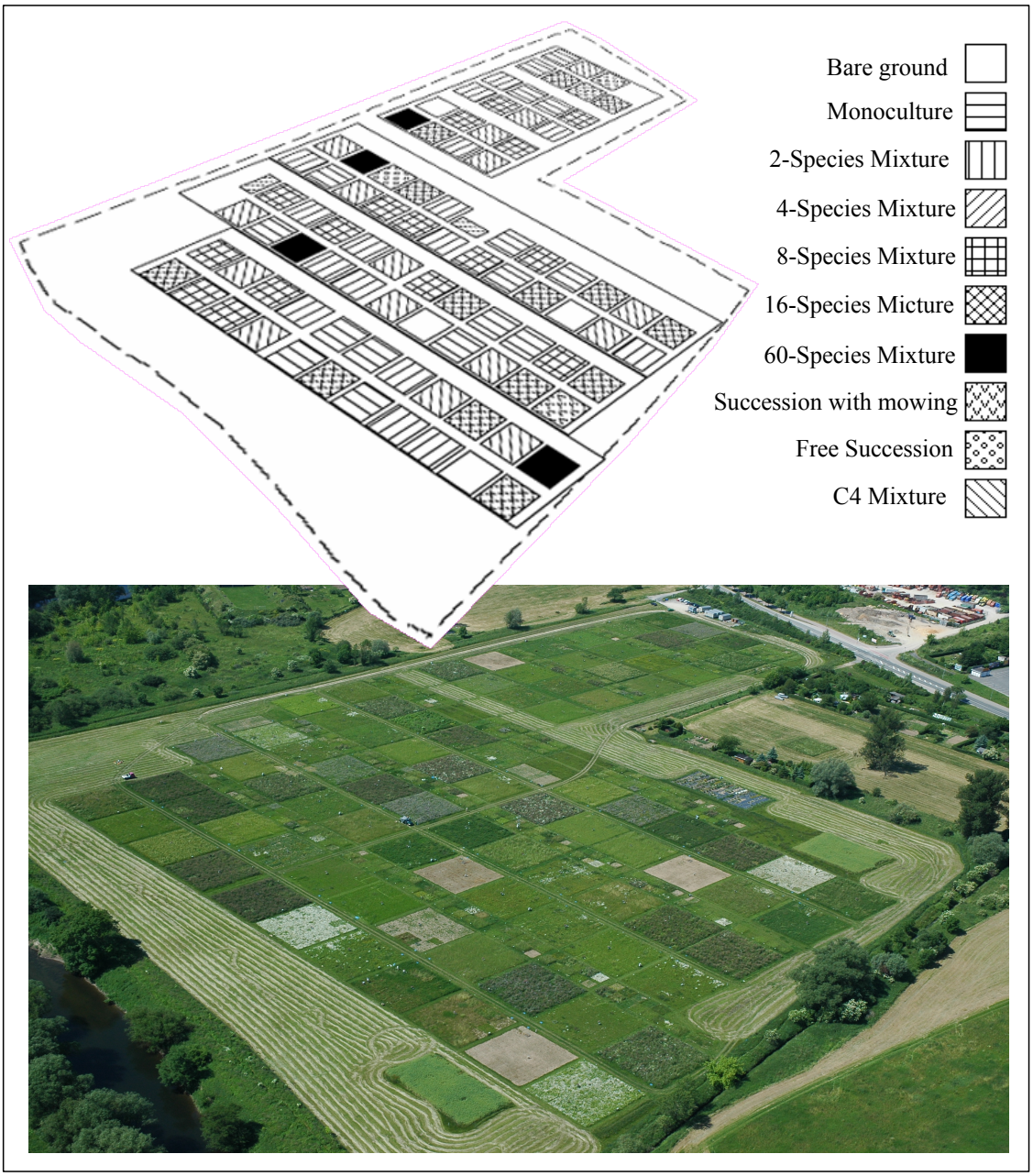

Figure 1.4 Photograph of the Jena Experiment field site located at the northern edge of the city of Jena (Thuringia, Germany; Photograph by W. Voigt) along with a scaled scheme of the experimental design delineating the four blocks and the various plant species diversity levels.

Based on the typical regional grassland vegetation the target plant community of the experiment represents Central European species-rich semi-natural mesophilic grassland (*Molinio-Arrhenatheretea* meadows, ***Arrhenatherion* community**; Ellenberg 1996) traditionally used as a hay meadow. The species pool consisted of 60 native plant species

which were assigned to the **four plant functional groups** grasses (GR; 16 species), small herbs (SH; 12 species), tall herbs (TH; 20 species), and legumes (LEG; 12 species) based on morphological, phenological and physiological traits using multivariate cluster analysis and ordination techniques (Fig. 1.5E; Roscher et al. 2004). To provide all possible combinations of plant species richness and number of plant functional groups, plant species were selected randomly with replacement from the species pool and sown out on 82 experimental plots to establish **gradients in plant species (1, 2, 4, 8, 16, and 60) and plant functional group richness (1, 2, 3, and 4;** Fig. 1.5A**)**. Seeds were obtained from commercial suppliers. To achieve the desired seedling density of 1000 equally divided seedlings per m^2, scarcely or not established species were resown in November 2002. In order to maintain the target plant community composition, the experimental plots were weeded twice a year in April and July (Fig. 1.5D). According to the typical management regime of extensively used mesophilic hay meadows, the plots were mown twice a year in June and September, and remained unfertilized throughout the experiment (Fig. 1.5B).

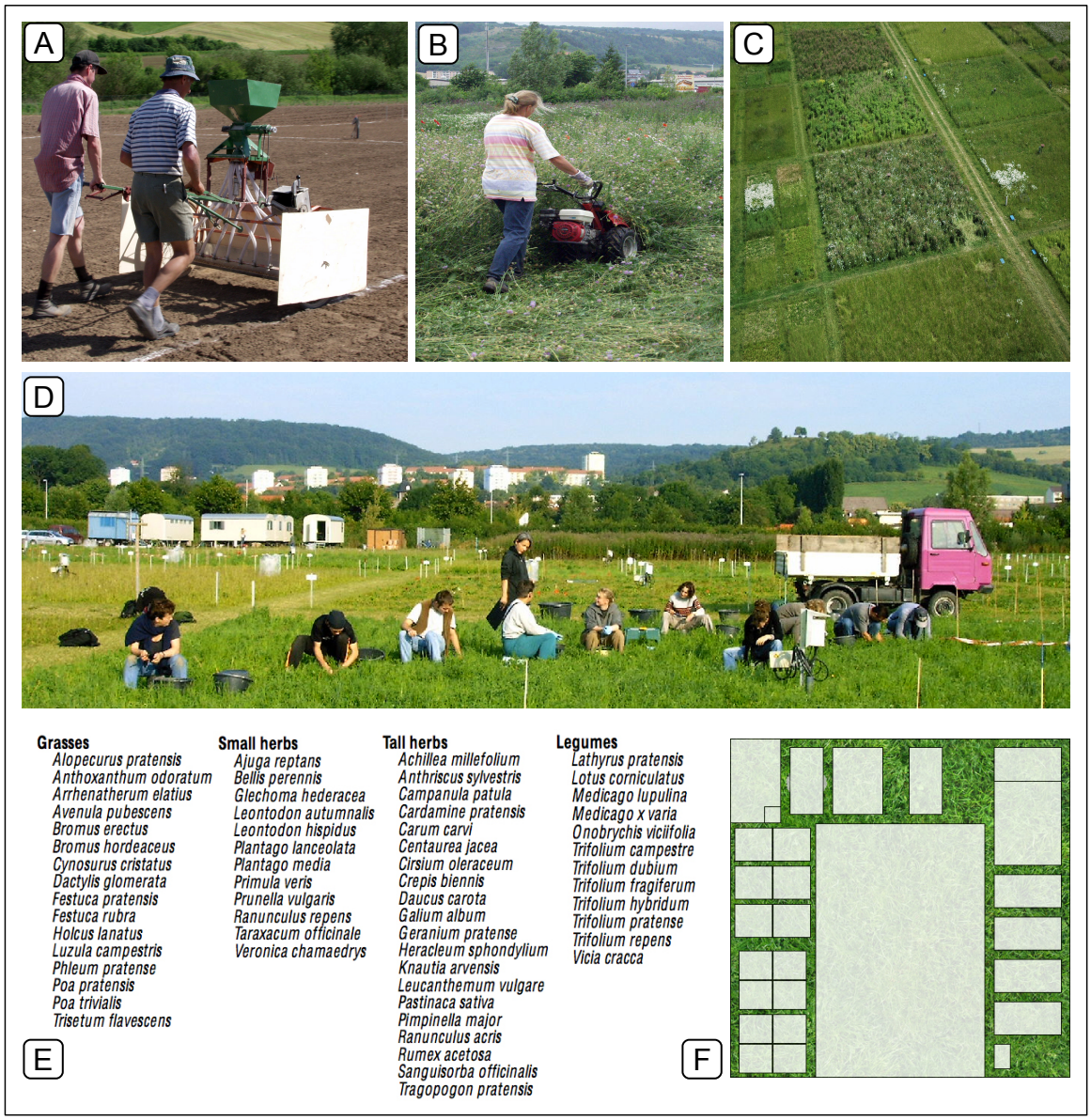

Figure 1.5 Impressions of the establishment and maintenance of the Jena Experiment. (**A**) Sowing of target plant species during the establishment of the main experimental plots. (**B**) Mowing of the field site in accordance with the typical management regime of the regional hay meadows. (**C**) Aerial view showing some of the main experimental plots along with some of the smaller plots serving as replicates of the experimental design. (**D**) Weeding of non-target plant species to maintain the targeted plant species communities. (**E**) Plant species pool of the Jena Experiment depicting the assignment of plant species to the four plant functional groups *grasses*, *small herbs*, *tall herbs*, and *legumes* (Roscher et al. 2004). (**F**) Layout of main experimental plot 'B1A01' detailing the nested subplots used by the various work groups involved in the Jena Experiment. (Photographs (**A**), (**B**) and (**D**) by Forschergruppe Biodiversität, Subproject Z; photograph (**C**) by W.Voigt)

1.4 TERRESTRIAL ECOSYSTEMS

Traditionally, terrestrial ecosystems have been separated into an above- and a belowground compartment. However, both subsystems are intimately linked by plants, which live in both spheres and therefore can be interpreted as the connecting unit between the above- and belowground system (Scheu 2001, Wardle et al. 2004). The **aboveground plant compartment** is responsible for the production of organic carbon, thereby forming the nutritional basis for above- and belowground biota, with the **belowground decomposer communit**y breaking down organic matter and mobilizing nutrients for plant uptake (Scheu and Setälä 2002, Wardle 2002, Wardle et al. 2004). Hence, plant growth largely depends on the activity of the decomposer community which, in turn, affects their own resource by increasing the availability of nutrients. Surprisingly, studies considering both subsystems are rare and the interrelationship between plant and soil animal communities is largely unknown. In fact, even though the majority of terrestrial animal taxa belong to the belowground decomposer community, the soil system is still one of the least investigated habitats of our planet (Wolters 2001, Coleman et al. 2004).

As soil organisms generally lack specified feeders, they are often classified according to body size, with bacteria and fungi (**microflora**) being the smallest size class of this system. They are followed by the **microfauna**, comprising organisms with less than 0.1 mm body size such as protozoa or nematodes, and by the **mesofauna**, consisting of e.g., **Collembola** or mites with a body width between 0.1 mm and 2 mm. Soil animals with body sizes exceeding 2 mm are classified as **macrofauna**, with earthworms and millipedes being the most prominent examples.

1.5 INTERACTIONS BETWEEN THE ABOVEGROUND AND BELOWGROUND SYSTEM

The soil animal community essentially relies on organic carbon sources such as plant residues and root exudates entering the soil system (Albers et al. 2006). Thus, species-rich plant communities are likely to provide a more diversified arrangement of carbon compounds and litter fragments which might increase the diversity of the belowground decomposer community (Hooper et al. 2000). However, as we will see in **Chapter 2**, traits of plant communities are subject to temporal variation and belowground properties vary with season

due to the different quality and quantity of resources entering the belowground system (Van der Putten et al. 2001, Habekost et al. 2008). Nevertheless, the decomposer community seems to be less responsive to variations in plant community composition than e.g., aboveground herbivores (Salamon et al. 2004, Wardle et al. 2004, Milcu et al. 2008). A possible explanation for this could be the low degree of food specialization within the soil animal community, with most decomposers being generalist feeders of dead organic matter (Maraun et al. 2003). The absence of co-evolution between soil decomposers and their basal food source could have abated the plant-decomposer-relationship.

Corresponding to the assertions of the singular hypotheses (q.v. Section 1.1 of this Chapter), the effect of different plant species or plant functional groups on ecosystem processes can vary dramatically (e.g., Spehn et al. 2002, Milcu et al. 2008). Therefore, it is indispensable to also consider the specific composition, i.e. the identity of plant species or plant functional groups, of a given community. The fact that some species exert a greater impact on certain ecosystem parameters than others becomes especially clear in the case of '**keystone species**' or '**ecosystem engineers**' such as e.g., legumes. Both terms refer to species whose presence or loss has a disproportionate impact on the community as compared to the presence or absence of other species. As an example, presence of legumes can have large-scale effects on nitrogen cycling. Due to their capability to fix atmospheric nitrogen, legumes greatly increase the amount of this essential plant nutrient in the soil (Spehn et al. 2002), thereby facilitating the establishment and growth of other (non-leguminous) plant species in their neighborhood. On the contrary, this nutrient enrichment may also encourage invasion of the plant community by fast growing grasses or other invasive species, subsequently reducing plant species richness and increasing susceptibility to environmental threats. While legumes are just one example of a 'keystone' plant functional group, there are other species whose addition or loss may have little or no effect on ecosystem processes.

1.6 COLLEMBOLA

Collembola (commonly known as “springtails”) are currently considered to be a monophyletic class at the base of the phylum Arthropoda, and even though they are usually treated as insects their exact taxonomic position is still subject of some debate. In fact, recent morphological and molecular evidence places them as a separate evolutionary lineage that branched off much earlier than the separation of many crustaceans and insects, making the

taxon Hexapoda paraphyletic (Nardi et al. 2003). Fossil records of Collembola date back to the early Devonian, about 400 million years ago, making them the oldest insects known on earth (Engel and Grimaldi 2004). Today, Collembola are present on every continent where they form a major component of terrestrial ecosystems, colonizing soils of temperate regions as well as sea shores (e.g., *Anurida maritima*; Hopkin 1997) or arid habitats like Australian sand deserts. They can even be found on the icy cover of Antarctica, where *Cryptopygus antarcticus* (Isotomidae) is one of the most common invertebrate species (Hopkin 2007). Several species like *Podura aquatica* live almost permanently on the surface of freshwater bodies while others like *Deuterosmithurus delatorrei* occupy dry forest canopies and are never found in the soil or litter layer (Palacios-Vargas and Gonzalez 1995). Until today, approximately 7000 species of Collembola have been described (Deharveng 2004) although the estimated total number is likely to be in the tens of thousands of species. Even though Collembola are primarily wingless they can be dispersed over large distances by wind. The most conspicuous morphological feature of Collembola is the furca, which evolved through the basal fusion of a pair of appendages on the fourth abdominal segment (Fig. 1.6C). It serves as a jumping organ, enabling the animals to bridge distances that span many times their own body length to evade predators. However, in order to ease their movement between soil particles or densely packed leaf litter, some edaphic (soil-dwelling) Collembola species have reduced the size of the furca, or even lost their jumping organ completely (Fig. 1.6B). Most Collembola species measure only a few millimeters in body length and are thus classified as mesofauna. They are usually poorly pigmented and live permanently in spaces between soil particles and in the litter layer. However, some epedaphic (surface-living) species can grow up to a length of 10 mm and show colorful pigmentation (Hopkin 2007; Fig. 1.6D, E).

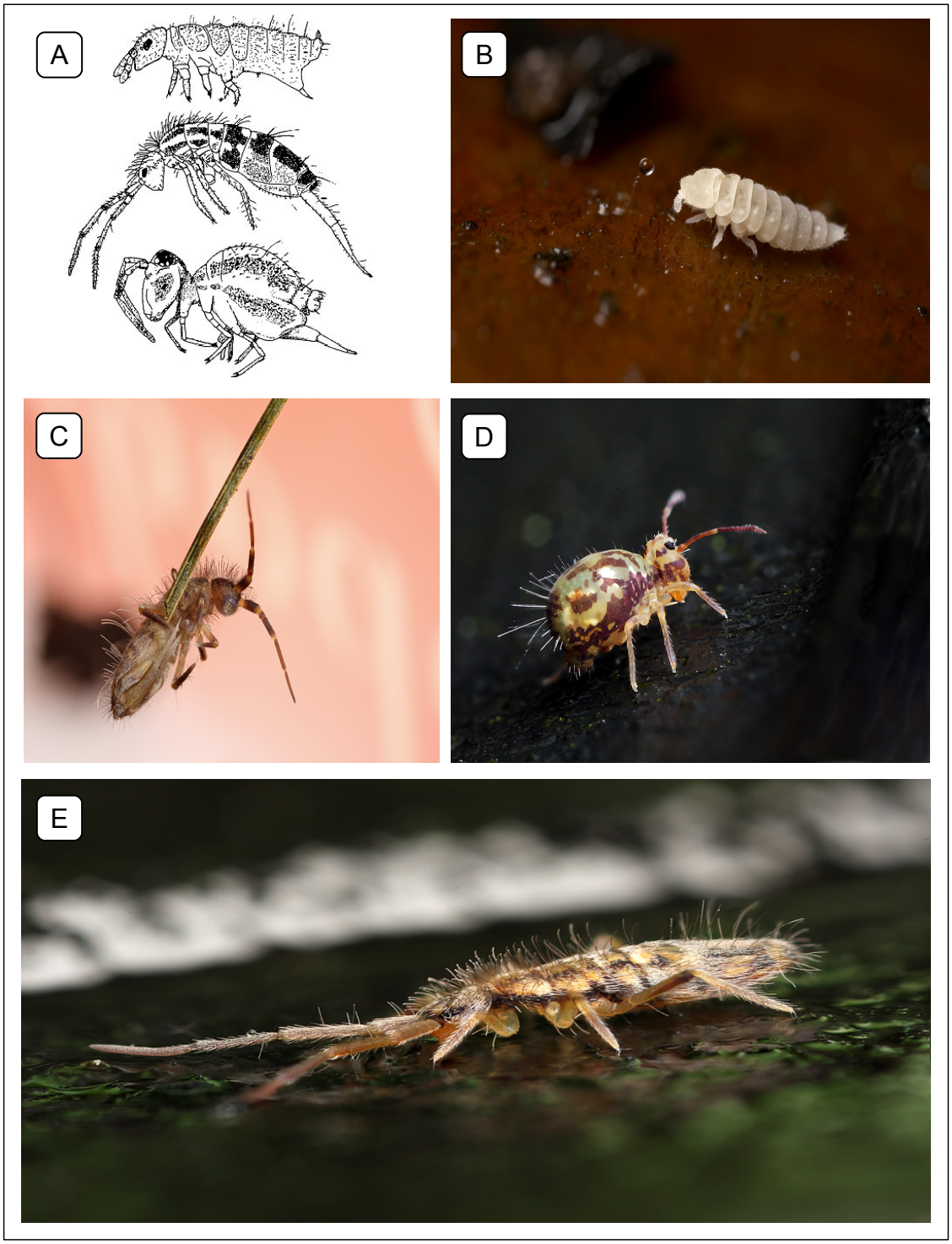

Figure 1.6 Diagram of the various forms of Collembola. (**A**) Scheme depicting the habitus of three representative species of the Collembola families Hypogastruridae, Entomobryidae, and Sminthuridae (top to bottom; adapted from Christiansen 1992). (**B**) *Kalaphorura burmeisteri* (Onychiuridae), an unpigmented blind species found under fallen branches or among leaf litter. (**C**) *Orchesella villosa* (Entomobryidae), distinctly showing the jumping organ (furca), ventral tubus, and retracted (entognathous) mouthparts within the head capsule. (**D**) *Dicyrtomina saundersi* (Dicyrtomidae), a richly pigmented globular springtail. (**E**) *Entomobrya intermedia* (Entomobryidae), showing its distinct pigmentation and hairs. All Photographs © Brian Valentine.

In terrestrial ecosystems, Collembola are particularly abundant in soil and in the litter layer. In grassland soils they can reach densities of up to 57,000 individuals/m^2 (Gange and Bower 1997) and up to 1 Mio individuals/m^2 in boreal coniferous forests (Petersen and Luxton 1982). They are generally considered to be saprophagous or microphytophagous feeding on soil fungi and dead organic matter (De Ruiter et al. 1993, Hopkin 1997). In fact, their diet has been shown to be more variable, with some species feeding on algae, bacteria, nematodes and living plant tissue (Rusek 1998, Chahartaghi et al. 2005, Ruess et al. 2005, Endlweber et al. 2009). Collembola may also graze on hyphae of mycorrhizal fungi (Moore et al. 1987), thereby influencing the mutualistic relationship between the plant and the fungus either positively or negatively, depending on the density of the animals (Finlay 1985, Harris and Boerner 1990, Gange 2000). By grazing on microorganisms and fungi in the rhizosphere of plants, Collembola are able to control population dynamics and activity of microorganisms and, thereby, the mineralization of nutrients essential for plant nutrition (Parkinson 1983, Filser 2002). The constant release of nutrients from Collembola faecal pellets has also been shown to beneficially affect plant nutrition (Sjursen and Holmstrup 2004). In fact, most soils contain millions of faecal pellets per square meter and an alpine soil type (alpine pitch rendzina on limestone) is composed almost entirely of Collembola faeces (Kubiena 1953).
As we will see in **Chapter 3**, Collembola are able to change the competitive relationship between plant species and alter the composition of plant communities by affecting plant nutrition either directly or indirectly (Kreuzer et al. 2004, Endlweber et al. 2006, Endlweber and Scheu 2007).

1.7 OBJECTIVES

The present thesis intends to explore the main mechanisms by which Collembola affect plant communities of varying species and functional group diversity and how plant communities of varying diversity in turn influence the belowground decomposer community. To implement this comprehensive approach it is necessary to combine field studies and greenhouse experiments performed under controlled conditions.

Using the experimental grassland community at the field site of the Jena Experiment, **Chapter 2** explores how the diversity and composition of the Collembola community are influenced by plant species richness, plant functional group richness and identity of plant

functional groups. Field studies investigating effects of plant diversity on Collembola are surprisingly rare and showed conflicting results (Edwards and Lofty 1974, Curry and Tuhoy 1978, Salamon et al. 2004). Moreover, these studies often neglected temporal changes of plant community effects on the belowground system. In order to extend current knowledge on the mechanisms structuring Collembola communities in the field, this experiment intended to assess whether

- Collembola community structure is affected by plant diversity four years after the establishment of the experimental plant community;
- increasing plant species and plant functional group richness beneficially affects Collembola density and diversity;
- presence of certain plant functional groups, in particular legumes, is more important than plant diversity *per se*;
- the impact of plant diversity and functional identity varies with season.

In addition to the field experiment focusing on temporal changes of plant community effects on Collembola, two greenhouse studies were conducted to elucidate effects of the Collembola community as well as interactive effects of Collembola and arbuscular mycorrhizal fungi on plant performance and competitive relationships between plants of different functional groups.

In **Chapter 3**, the influence of Collembola diversity on plant growth and decomposition processes was investigated. Recent studies on effects of soil arthropods on plant performance mainly focused on the presence and density of Collembola, thereby neglecting effects of species richness and interspecific interactions, such as competition and facilitation. Building on these studies, this greenhouse experiment intended to assess how plant productivity and decomposition processes are influenced by Collembola diversity and if effects of Collembola vary with plant functional group identity. Specifically, we asked whether

- presence of Collembola beneficially affects plant performance and litter decomposition;
- plant productivity increases with increasing Collembola diversity due to complementary interactions among different Collembola species;
- Collembola performance varies with diversity and plant functional group identity.

In **Chapter 4**, we investigated effects of Collembola and **arbuscular-mycorrhizal fungi (AMF)** on plant competition and the performance of three grassland plant species representing three dominant plant functional groups (grasses, legumes and herbs). Further, we investigated variations in Collembola performance and AMF colonization rates of plant roots as influenced by the different plant communities. Even though mycorrhizal fungi and Collembola are known to influence plant nutrition and therefore plant competition, surprisingly little is known about interactive effects on plant performance. However, Collembola play an important role in the interrelationship between mycorrhizal fungi and their host plants (Klironomos and Kendrick 1996) and are likely to influence competitive relationships within plant communities. Thus, the objectives of this greenhouse experiment were to identify if

- Collembola performance and mycorrhizal colonization vary with plant species;
- Collembola and AMF interactively affect plant nutrition and growth;
- effects of Collembola and AMF vary depending on plant species, resulting in changes in the competitive strength of certain plant species.

The results of all experiments are discussed in **Chapter 5** to provide an integral synopsis of the role of Collembola in terrestrial ecosystems. By considering the observations of the single experiments of this thesis as well as those from other authors, the interactions between Collembola and plant communities of varying species and functional group diversity are described in a holistic way to provide perspectives for future research in the field of biodiversity and ecosystem processes.

Chapter 2

Impacts of Plant Diversity and Functional Group Identity on Collembola Communities vary with Season

2.1 ABSTRACT

Declining biodiversity is one of the most important aspects of anthropogenic global change phenomena, but the implications of plant species loss for soil decomposers are little understood. We used the experimental grassland community of the Jena Experiment to assess the response of density and diversity of Collembola to varying plant species richness, plant functional group richness and plant functional group identity. We sampled the experimental plots in spring and autumn four years after establishment of the experimental plant communities.

Collembola density and diversity significantly increased with plant species and plant functional group richness highlighting the importance of the singular hypothesis for soil invertebrates. Generally, grasses and legumes beneficially affected Collembola density and diversity, whereas effects of small herbs usually were detrimental. These impacts were largely consistent in spring and autumn. By contrast, in the presence of small herbs the density of hemiedaphic Collembola and the diversity of Isotomidae increased in spring whereas they decreased in autumn.

Beneficial impacts of plant diversity as well as those of grasses and legumes were likely due to increased root and microbial biomass, and elevated quantity and quality of plant residues serving as food resources for Collembola. By contrast, beneficial impacts of small herbs in spring probably reflect differences in microclimatic conditions, and detrimental effects in autumn likely were due to low quantity and quality of resources.

The results point to an intimate relationship between plants and the diversity of belowground biota, even at small spatial scales, contrasting the findings of previous studies. The pronounced response of soil animals in the present study was presumably due to the fact that plant communities had established over several years. As decomposer invertebrates significantly impact plant performance, changes in soil biota density and diversity are likely to have major feedbacks on plant community productivity and composition.

2.2 INTRODUCTION

Human activities such as land transformation, homogenization of habitats, biotic exchange, and nitrogen and CO2 depositions have caused a worldwide decline in species richness (Vitousek et al. 1997, Sala et al. 2000). Since biodiversity is known to affect a variety of ecosystem functions (Schulze and Mooney 1994, Loreau et al. 2002), an increasing number of studies focused on biodiversity impacts on ecosystem processes. Several studies highlighted the positive relationship between plant diversity and aboveground productivity (Naeem et al. 1994, Roscher et al. 2005). However, there still is a lack of knowledge on the relationship between plant diversity and belowground properties such as soil structure or soil community composition (Koricheva et al. 2000, Gastine et al. 2003, Hedlund et al. 2003). In contrast to aboveground plant productivity, the response of the belowground system, including that of soil biota, presumably is more complex and context dependent (Hooper et al. 2000, Wardle 2002, Wardle et al. 2004). While belowground responses related to increasing plant diversity often are absent or idiosyncratic (Wardle et al. 1999, Gastine et al. 2003, Hedlund et al. 2003, Milcu et al. 2008), some studies also reported positive effects on decomposition processes (Spehn et al. 2000), nutrient availability (Oelmann et al. 2007), and the density and diversity of the soil fauna (Spehn et al. 2000, Haddad et al. 2001, Porazinska et al. 2003, De Deyn et al. 2004, Milcu et al. 2008, Viketoft et al. 2009). In addition, presence of key plant functional groups, such as legumes, has often been reported to strongly affect the decomposer subsystem by altering resource quality and quantity (Habekost et al. 2008, Milcu et al. 2008, Eisenhauer et al. 2009). However, most studies investigating the relationship between plant diversity and soil fauna focussed on certain animal groups in particular earthworms (Milcu et al. 2008, Eisenhauer et al. 2008) or insect herbivores (Haddad et al. 2001), and neglected the response of other important groups of the soil decomposer system.

Collembola constitute a fundamental component of the soil mesofauna (Bardgett and Cook 1998, Rusek 1998) with densities up to 57,000 individuals/m^2 in grassland soils (Gange and Bower 1997). They are generally considered to predominantly feed on soil fungi (Hopkin 1997, Coleman et al. 2004), albeit this view is oversimplified; in fact Collembola feed on a great variety of diets including algae, dead organic matter, living plant tissue and nematodes (Rusek 1998, Chahartaghi et al. 2005, Ruess et al. 2005). An analysis of the digestive enzymes in Collembola showed more chitinase than trehalase and cellulose activity suggesting that Collembola feed on fungi, but also have the ability to digest plant materials

(Berg et al. 2004). By affecting the biomass and activity of soil microorganisms either directly via feeding on fungi and bacteria (Bakonyi 1989, Bardgett et al. 1993a) or indirectly, e.g., via dissemination of microbial propagules and alteration of nutrient availability (Griffiths and Bardgett 1997), Collembola can control the population dynamics of soil microorganisms (Parkinson 1983, Filser 2002). Since nutrient mineralization is essentially driven by microbial activity (Schlesinger 1977, Swift et al. 1979), Collembola play an important role in decomposition processes (Cragg and Bardgett 2001, Cole et al. 2006). Hence, Collembola activity is likely to feed back to primary producers, as producers depend on the nutrients made available by microorganisms and decomposer animals (Filser 2002, Bardgett 2005). Surprisingly, field studies investigating effects of plant diversity on Collembola are rare and often show conflicting results. Some studies suggested plant diversity to be of little importance for Collembola diversity (Curry and Tuhoy 1978, Salamon et al. 2004), whereas Edwards and Lofty (1974) reported a positive relationship. The decomposer system is generally thought to be mainly driven by presence of certain plant functional groups, such as legumes and grasses, rather than by plant species richness (Spehn et al. 2000, Habekost et al. 2008, Milcu et al. 2008). In contrast to this view, a recent field study on soil microbial communities and functions highlighted the importance of the singular hypothesis of plant diversity by indicating that plant species are unique, each contributing to the functioning of the belowground system (Eisenhauer et al., 2010a). Interestingly, this study showed that after a time-lag of about four years plant species richness was the most important plant community property affecting soil microorganisms, and the effect did not rely on plant productivity or the presence of certain plant functional groups.

Plant community characteristics are subject to temporal variation (Van der Putten et al. 2001). This is particularly true for aboveground attributes like vegetation structure or microclimatic conditions. Moreover, belowground properties also vary with season due to the different quality and quantity of resources entering the belowground system, thus altering the microbial community during the course of the year (Habekost et al. 2008). Since decomposers are linked to the soil microbial community and depend on resource input from the aboveground system, plant community effects on Collembola likely vary with season.

The present study was conducted to examine the effects of plant species richness, plant functional group richness and presence of certain plant functional groups on the density and diversity of Collembola in Central European grassland. To assess if plant diversity impacts are transient, i.e. vary with season, we sampled Collembola in spring and in autumn.

In order to study well established plant communities, we sampled four years after the set-up of the experimental plots. We hypothesized that (1) increasing plant species and plant functional group richness beneficially affects Collembola density and diversity, (2) presence of certain plant functional groups, in particular legumes, is more important than plant diversity per se.

2.3 MATERIALS AND METHODS

SITE DESCRIPTION AND EXPERIMENTAL DESIGN

The present study was conducted as part of the Jena Experiment, a large biodiversity experiment located in the floodplain of the Saale river (altitude 130 m asl) at the northern edge of the city of Jena (Thuringia, Germany; Roscher et al. 2004). The soil is an Eutric Fluvisol (FAO-Unesco 1997), mean annual air temperature 3 km south of the field site is 9.3 °C and mean annual precipitation is 587 mm (Kluge and Müller-Westermeier, 2000). Formerly used as an arable field for vegetables and wheat, the site was ploughed and harrowed several times before the establishment of the experiment in May 2002. The target plant community represents Central European semi-natural grassland (Arrhenatherion community; Ellenberg 1996) according to the regional grass- land vegetation. The species pool consisted of 60 native plant species (Table 2.1), which were assigned to the four plant functional groups: grasses (16 species), small herbs (12 species), tall herbs (20 species), and legumes (12 species) according to morphological, phenological and physiological traits using multivariate cluster analysis (see Roscher et al. 2004 for detailed species list and allocation of species to functional groups). To provide all possible combinations of plant species richness and number of plant functional groups, plant species were selected randomly with replacement from the species pool and sown on 82 experimental plots of 20 x 20 m to establish a plant species (1, 2, 4, 8, 16, and 60) and plant functional group (1, 2, 3, and 4) richness gradient (Table 2.1) which was maintained by weeding of the field site twice a year (April and July). According to the management regime of regional hay meadows, the plots were mown twice a year (June and September), but remained unfertilized throughout the experiment. The plots were grouped into four blocks parallel to the Saale river to account for changing soil characteristics with increasing distance from the river, mainly stone surface cover (0-23%), sand content (45-628 g/kg) and $CaCO_3$ concentration (40-391 g/kg). Thus,

effects of soil heterogeneity can be separated from biodiversity effects in the statistical analysis. Each block contained a virtually equal number of plots (20-21 plots), plant species (four replicates of each plant species richness level with the exception of 16 species mixtures (3-4 replicates) and 60 species mixtures (1 replicate)) and plant functional group diversity levels.

Table 2.1 Design of the Jena Experiment. Combinations of plant species richness (SR) and plant functional group richness (FR) and the number of replicates per diversity level (given in italics). For more details on the experimental design see Roscher et al. (2004).

		SR						
		1	2	4	8	16	60	Replicates
FR	1	*16*	*8*	*4*	*4*	*2*	-	*34*
	2	–	*8*	*4*	*4*	*4*	–	*20*
	3	–	–	*4*	*4*	*4*	–	*12*
	4	–	–	*4*	*4*	*4*	*4*	*16*
Replicates		*16*	*16*	*16*	*16*	*14*	*4*	
								82 plots

SAMPLING AND IDENTIFICATION OF COLLEMBOLA

Collembola were sampled by sequential soil core sampling to a depth of 10 cm in May and November 2006 (i.e. four years after establishment of the experimental plant communities) to account for seasonal variations (Bardgett et al. 1993a). Soil sampling was performed using a steel corer (diameter 5 cm) two and ten weeks after the first and second mowing of the experimental plots, respectively (Fig. 2.1). One soil core per plot was taken at a pre-defined position (which had not been sampled before; distance between sampling locations of different plots >5 m), and Collembola were extracted by heat (Kempson et al. 1963), collected in diluted glycerol and transferred into ethanol (70%) for storage. Collembola were determined to species level following Gisin (1960), Fjellberg (1998, 2007), Hopkin (2007) and counted. Small specimens were mounted on slides and identified using a compound microscope under phase contrast illumination. The numbers obtained served as

abundance measures and were summed up and assigned to the following Collembola taxa: total Collembola, Entomobryidae, Isotomidae, Onychiuridae, Hypogastruridae and Sminthuridae. Juvenile Collembola which could not be assigned to one of the taxa were included in total Collembola in the statistical analysis. Additionally, those Collembola taxa identified to species level were ascribed to the life history groups epedaphic (litter dwelling), euedaphic (soil dwelling), hemiedaphic and hemi- to epedaphic (intermediate, litter to soil dwelling species; Gisin 1943, Hopkin 2007) to consider the response of Collembola differing in functional traits to manipulations of plant community composition (Table 2.2). For characterization of Collembola diversity and dominance structure, Collembola species number and the Shannon-Wiener diversity index were calculated (Shannon 1948, Shannon and Weaver 1949).

Figure 2.1 Photographs demonstrating Collembola sampling at the Jena Experiment field site using a steel corer (Photographs by A. Sabais).

STATISTICAL ANALYSES

Sequential split-plot analysis of variance (ANOVA) as part of the general linear model (GLM, type I sum of squares) was performed to analyze the effects of block (soil heterogeneity), (sown) plant species richness (log-transformed), plant functional group richness, presence of grasses, small herbs, tall herbs and legumes, plot, season (sampling times were represented by subplots in the split- plot ANOVA) and interactions between season and plant community parameters on the density and diversity of total Collembola, Entomobryidae, Isotomidae, Onychiuridae, Hypogastruridae and Sminthuridae as well as on the life history groups epedaphic, euedaphic, hemiedaphic and hemi- to epedaphic. Since plant species richness and plant functional group richness are partially linked (Table 2.1; Roscher et al. 2004), no interaction between these two factors was analyzed. Treatments analyzed at the plot scale (block, plant species richness, plant functional group richness, grasses, legumes) were tested against the variance between plots to avoid pseudoreplication, whereas treatments analyzed at the subplot scale (season and interactions) were tested against the total variance (Scheiner and Gurevitch 2001). The split-plot approach was chosen due to the fact that we sampled the same plots in spring and autumn, i.e. samples derived from one plot were not independent from each other. After fitting the full model, the respective models were optimized by excluding non-significant factors using the Akaike information criterion (AIC, not shown; Burnham and Anderson 1998) and by testing plant species richness and plant functional group richness either as categorical or as continuous factors in separate models. Plant species richness was always fitted as a continuous factor in the final models.

F-values given in text and tables refer to those where the respective factor and interaction was fitted first (Schmid et al. 2002). Block was always fitted first to remove the variance caused by soil abiotic heterogeneity at the experimental field site, followed by plant species richness and plant functional group richness. Thereafter, the effects of presence of certain plant functional groups were calculated (whose sequence was alternated). Statistical analyses were performed using SAS V9.2 (SAS Institute Inc., Cary, USA). We did not correct for multiple statistical tests considering the mathematical and logical argumentation by Moran (2003). To meet the requirements of ANOVAs (normal distribution and homogeneity of variances) data were log (x + 1) transformed. Means (± standard error) presented in text and figures were calculated using non-transformed data.

2.4 RESULTS

COLLEMBOLA COMMUNITY STRUCTURE

The Collembola community consisted of 26 species belonging to the families Entomobryidae, Isotomidae, Onychiuridae, Hypogastruridae and Sminthuridae (Fig. 2.2A) and the life history groups epedaphic, hemiedaphic and euedaphic (Fig. 2.2B; Table 2.2). The most abundant species were *Lepidocyrtus cyaneus* (Tullberg 1871), *Heteromurus nitidus* (Templeton, 1835), *Pseudosinella alba* (Packard, 1873), Isotoma viridis (Bourlet, 1839), and *Parisotoma notabilis* (Schäffer, 1896). On average, 5988 individuals per m^2 were extracted in spring, and 13,857 individuals per m^2 in autumn (averaged over all plots), with the difference being statistically significant (Tables 2.2-2.4). Generally, soil abiotic parameters (block) strongly affected Collembola density and diversity (Tables 2.2-2.4); however, block effects are not discussed here as we focused on biotic rather than abiotic drivers of Collembola community composition.

EFFECTS OF PLANT DIVERSITY

Overall, plant species richness had the strongest and most consistent impact on Collembola density and diversity (all positive effects; Tables 2.2-2.4). Total Collembola density increased significantly with increasing plant species richness (Fig. 2.2A) which was mainly due to changes in the density of Entomobryidae, Isotomidae and Onychiuridae as well as the life history groups euedaphic, hemiedaphic and hemi- to epedaphic (Table 2.2). Similarly, Collembola density increased with increasing plant functional group richness, particularly the families Entomobryidae and Onychiuridae as well as the life history group comprising hemi- to epedaphic species (Table 2.2). Generally, the impacts of plant diversity measures were largely consistent between seasons; however, the density of Onychiuridae increased significantly with increasing plant species and functional group richness in spring but not in autumn (Table 2.2).

Table 2.2
GLM table of *F*-values for the effects of Block (BL), plant species richness (SR), plant functional group richness (FR), presence of grasses (GR), small herbs (SH), tall herbs (TH), and legumes (LE), plot, season (SS) and interactions between SE and plant community parameters on the density of total Collembola, Entomobryidae, Isotomidae, Onychiuridae, Hypogastruridae and Sminthuridae, as well as on the Collembola life history groups epadephic, euedaphic, hemiedaphic and hemi- to epedaphic. "% Significant" gives the percentage of variables significantly affected by the respective factor.

	Factors plot-level							*Plot*	Factors subplot-level							*Error*
	BL	SR	FR	GR	SH	TH	LE		SS	SS × SR	SS × FR	SS × GR	SS × SH	SS × TH	SS × LE	
Collembola total	4.73**	**4.02***	**4.03***	0.89	excl	3.58	2.86	*1.11*	**20.73*****	1.76	1.86	1.33	excl	excl	excl	*72/77*
Families																
Entomobryidae	3.76*	**4.56***	**5.00***	excl	excl	1.48	1.69	*0.91*	**23.94*****	excl	excl	excl	excl	excl	excl	*73/80*
Isotomidae	3.02*	**4.54***	2.76	1.47	0.86	excl	excl	*1.33*	2.64	excl	excl	1.04	3.04	excl	excl	*73/78*
Onychiuridae	3.26*	**8.29****	**3.32*[f]**	0.94	1.15	excl	2.76	*1.06*	**103.06*****	**12.28*****	**3.89***	excl	1.56	excl	excl	*70/75*
Hypogastruridae	3.61*	excl	1.58	2.90	**3.95***	3.24	2.30	*2.10***	**6.72***	excl	1.08	2.67	excl	excl	3.61	*73/77*
Sminthuridae	4.17**	1.67	1.97	excl	excl	excl	excl	*0.95*	**4.21***	excl	excl	excl	excl	excl	excl	*75/80*
Life history groups																
Epedaphic	5.48**	excl	1.51	excl	0.48	excl	excl	*0.69*	2.52	excl	1.39	excl	2.83	excl	excl	*75/78*
Euedaphic	4.53**	**5.54***	2.19	1.08	3.23	excl	**4.56***	*0.69*	**14.59*****	excl	excl	excl	excl	excl	excl	*72/80*
Hemiedaphic	3.75*	**5.52***	excl	excl	0.81	1.96	0.13	*1.35*	1.49	1.30	excl	excl	**5.54***	excl	1.57	*73/77*
Hemi- to epedaphic	3.38*	**5.68***	**6.26***	3.78	1.90	2.85	1.22	*1.39*	**8.47****	excl	excl	excl	excl	excl	excl	*72/80*
% Significant		70%	40%	0%	10%	0%	10%		70%	10%	10%	0%	10%	0%	0%	

Significant effects ($P < 0.05$) are given in bold (effects of BL and Plot are not highlighted); error terms are given in italics. Degrees of freedom (df): BL = 3, SR = 1, FR = 1 (3^f), GR = 1, SH = 1, TH = 1, LE = 1, df *Plot* is given as the first number on the *Error* column, df total *Error* is given as the second number in the *Error* column.
Annotations: excl = excluded in the final statistical model based on AIC; [f] = categorical factor; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Table 2.3
GLM table of *F*-values for the effects of Block (BL), plant species richness (SR), plant functional group richness (FR), presence of grasses (GR), small herbs (SH), tall herbs (TH), and legumes (LE), plot, season (SS) and interactions between SE and plant community parameters on the species richness of total Collembola, Entomobryidae, Isotomidae and Onychiuridae, as well as on the Collembola life history groups euedaphic, hemiedaphic and hemi- to epedaphic. "% Significant" gives the percentage of variables significantly affected by the respective factor.

	Factors plot-level							*Plot*	Factors subplot-level							*Error*
	BL	SR	FR	GR	SH	TH	LE		SS	SS × SR	SS × FR	SS × GR	SS × SH	SS × TH	SS × LE	
Collembola total	5.36**	**10.16****	2.88	excl	**6.33***	1.14	1.15	*1.17*	**30.40*****	excl	2.52	excl	excl	excl	2.36	*72/78*
Families																
Entomobryidae	2.18	**11.80*****	**6.52***	excl	1.95	excl	1.90	*0.97*	**21.85*****	excl	excl	excl	excl	excl	excl	*73/80*
Isotomidae	2.29	2.06	excl	0.26	2.61	excl	0.15	*1.09*	**3.96***	excl	excl	2.03	**5.36***	excl	1.25	*73/77*
Onychiuridae	4.01*	**5.53***	1.14	1.97	1.69	excl	**4.64***	*1.18*	**71.78*****	**9.52****	**6.20***	excl	excl	excl	excl	*72/78*
Hypogastruridae	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
Sminthuridae	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
Life history groups																
Epedaphic	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
Euedaphic	3.06*	**4.87***	1.36	1.95	**5.48***	1.68	**5.51***	*1.02*	**15.15*****	excl	excl	excl	excl	excl	excl	*72/80*
Hemiedaphic	excl	**3.96***	excl	excl	2.41	excl	excl	*1.41*	1.08	**5.34***	excl	excl	excl	excl	excl	*78/78*
Hemi- to epedaphic	3.26*	**6.47***	**4.01***	**4.50***	**6.75***	excl	excl	*1.44*	1.80	excl	1.31	excl	excl	excl	excl	*73/79*
% Significant		86%	29%	14%	57%	0%	29%		71%	29%	14%	0%	14%	0%	0%	

Significant effects ($P < 0.05$) are given in bold (effects of BL are not highlighted); error terms are given in italics. Degrees of freedom (df): BL = 3, SR = 1, FR = 1, GR = 1, SH = 1, TH = 1, LE = 1, df *Plot* is given as the first number on the *Error* column, df total *Error* is given as the second number in the *Error* column.
Annotations: excl = excluded in the final statistical model based on AIC; nc = not calculated; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Table 2.4
GLM table of *F*-values for the effects of Block (BL), plant species richness (SR), plant functional group richness (FR), presence of grasses (GR), small herbs (SH), tall herbs (TH), and legumes (LE), plot, season (SS) and interactions between SE and plant community parameters on the Shannon-Wiener index of diversity of total Collembola, Entomobryidae, Isotomidae and Onychiuridae, as well as on the Collembola life history groups euedaphic, hemiedaphic and hemi- to epedaphic. "% Significant" gives the percentage of variables significantly affected by the respective factor.

	Factors plot-level							*Plot*	Factors subplot-level							*Error*
	BL	SR	FR	GR	SH	TH	LE		SS	SS × SR	SS × FR	SS × GR	SS × SH	SS × TH	SS × LE	
Collembola total	4.74**	**8.46****	**4.10***	0.41	2.32	excl	0.56	*1.24*	**25.46*****	excl	excl	**4.80***	excl	excl	1.10	*72/78*
Families																
Entomobryidae	excl	**14.46*****	**5.16***	excl	2.48	excl	2.83	*0.87*	**15.67*****	excl	excl	excl	excl	excl	excl	*76/80*
Isotomidae	2.12	excl	2.10	1.40	1.80	excl	0.15	*0.77*	1.79	excl	excl	1.50	**5.15***	excl	3.20	*71/77*
Onychiuridae	3.42*	0.77	0.56	2.17	1.73	excl	**4.20***	*0.97*	**22.68*****	1.24	1.53	1.67	excl	excl	excl	*72/76*
Hypogastruridae	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
Sminthuridae	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
Life history groups																
Epedaphic	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
Euedaphic	excl	3.57	excl	1.46	**6.26***	1.48	0.99	*1.02*	**6.67***	1.11	excl	2.06	3.81	0.95	2.44	*75/75*
Hemiedaphic	excl	1.02	excl	excl	2.77	excl	0.01	*1.11*	2.43	excl	excl	excl	0.73	excl	1.94	*77/78*
Hemi- to epedaphic	1.73[f]	**5.13***	2.64	**4.68***	**8.65****	2.18	0.52	*1.32*	0.01	excl	1.09	1.14	1.87	1.67	1.23	*72/76*
% significant		43%	29%	14%	29%	0%	14%		57%	0%	0%	14%	14%	0%	0%	

Significant effects ($P < 0.05$) are given in bold (effects of BL are not highlighted); error terms are given in italics. Degrees of freedom (df): BL = 3, SR = 1, FR = 1, GR = 1, SH = 1, TH = 1, LE = 1, df *Plot* is given as the first number on the *Error* column, df total *Error* is given as the second number in the *Error* column.
Annotations: excl = excluded in the final statistical model based on AIC; nc = not calculated; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

There was an intimate positive relationship between plant diversity and Collembola diversity (Tables 2.3 and 2.4). Again, this was more pronounced for plant species richness than for plant functional group richness. Species richness of total Collembola (Fig. 2.2B), Entomobryidae and Onychiuridae as well as that of the life history groups euedaphic, hemiedaphic and hemi- to epedaphic increased significantly with increasing plant species richness (Table 2.3). By contrast, only the species richness of Entomobryidae and hemi- to epedaphic species increased significantly with increasing plant functional group richness (Table 2.3). Moreover, the Shannon-Wiener diversity index of total Collembola increased significantly with increasing plant species (Fig. 2.2C) and functional group richness which was mainly due to changes in the diversity of Entomobryidae and hemi- to epedaphic species (Table 2.4). Similar to Collembola density, the impact of plant diversity on Collembola diversity was largely consistent between seasons; however, the increase in the diversity of Onychiuridae and hemiedaphic species with increasing plant diversity was more pronounced in spring than in autumn.

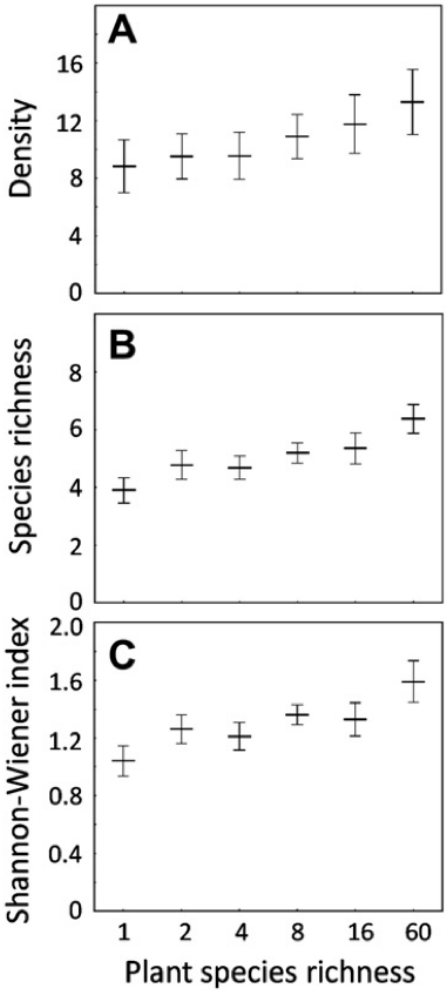

Figure 2.2 Relationship between plant species richness and (**A**) total Collembola density [individuals per m^2] ($P < 0{,}05$), (**B**) species richness per soil core (diameter 5 cm; $P < 0{,}01$), and (**C**) Shannon-Wiener index of diversity ($P < 0.01$). Means with standard error.

EFFECTS OF PLANT FUNCTIONAL GROUP IDENTITY

Generally, impacts of the presence of certain plant functional groups inconsistently affected Collembola density and diversity. The density of Hypogastruridae decreased significantly in the presence of small herbs (-45%) whereas the density of euedaphic Collembola increased in the presence of legumes (+214%), and the impact of small herbs on the density of hemiedaphic species varied between seasons being positive in spring (+104%) but negative in autumn (-62%; Table 2.2). Total Collembola species richness decreased significantly in the presence of small herbs (-10%); that of Isotomidae increased in spring (+10%) but decreased in autumn in the presence of small herbs (-33%); that of Onychiuridae increased in the presence of legumes (+21%); that of euedaphic species decreased in the presence of small herbs (-19%), while it increased in the presence of legumes (+43%; Table 2.3). Moreover, the richness of hemi- to epedaphic species decreased significantly in the presence of small herbs (-11%) while it increased significantly in the presence of grasses (+39%).

The Shannon-Wiener index of Collembola diversity increased considerably in the presence of grasses in spring (+41%), whereas it increased slightly in autumn (+4%; Table 2.4). Moreover, while the Shannon-Wiener index of Isotomidae diversity increased slightly in the presence of small herbs in spring (+7%), it decreased considerably in autumn (-68%). Similar to species richness of Onychiuridae, the Shannon-Wiener index of Onychiuridae diversity increased significantly in the presence of legumes (+22%). In line with species richness of euedaphic species, the Shannon-Wiener index of diversity decreased significantly in the presence of small herbs (-43%). Moreover and similarly to the results on species richness, the Shannon-Wiener index of diversity of hemi- to epedaphic species decreased significantly in the presence of small herbs (-23%), while it increased significantly in the presence of grasses (+66%).

2.5 DISCUSSION

During the last decade it has been increasingly recognized that changes in plant diversity may strongly affect the belowground system (Wardle et al. 2004), with the interrelationship being mainly investigated in grasslands (e.g. Siemann et al. 1998, Koricheva et al. 2000, Haddad et al. 2001, Salamon et al. 2004). However, most of these experiments focused on community- and ecosystem-level consequences of biodiversity decline, in particular on aboveground arthropods and a number of authors requested the investigation of long-term effects on decomposers (Tilman et al. 2001, Hedlund et al. 2003, Viketoft et al. 2009, Eisenhauer et al. 2010a).

EFFECTS OF PLANT DIVERSITY

Consistent with our hypothesis (1), increasing plant species and plant functional group richness beneficially affected the density of most Collembola taxa and overall Collembola diversity. Remarkably, in terms of strength and consistency, impacts of plant species richness were more important than those of plant functional group richness. Plant species richness affected Collembola density and species richness in 70% and 86% of the cases, respectively. By contrast, respective values for plant functional group richness were only 40% and 29%. Moreover and in contrast to previous research on earthworms on the same field site (Eisenhauer et al. 2009c), the response of Collembola to variations in plant species richness was largely consistent between seasons (as indicated by the low number of significant interactions between season and plant community parameters; Tables 2.2-2.4). Particularly, the most abundant Collembola families Entomobryidae, Isotomidae and Onychiuridae as well as the life history groups euedaphic, hemiedaphic and hemi- to epedaphic species responded to plant diversity, resulting in highly significant positive relationships between plant diversity and total Collembola density and diversity. The lack of plant diversity effects on epedaphic Collembola was likely due to the fact that only one species of low abundance (*Sminthurinus niger*) could be assigned to this life history group. Results of hemi- to epedaphic Collembola indicate that surface-active species are also affected by plant diversity, presumably due to variations in plant litter quality with plant diversity. This is consistent with the response of anecic earthworms feeding on the soil surface, which were also significantly affected by plant community parameters at the Jena Experiment field site (Eisenhauer et al. 2009c). In contrast, the impact of plant species richness on euedaphic species points to the importance of

belowground plant inputs, i.e. root litter and exudates, for belowground community structure and functioning as previously suggested (Milcu et al. 2006, Pollierer et al. 2007, Eisenhauer et al. 2009b).

The intimate relationship between plant diversity and Collembola diversity and density found here contrasts with results of previous experiments (Spehn et al. 2000, Salamon et al. 2004, Milcu et al. 2006). In the study of Spehn et al. (2000) Collembola responded inconsistently to increasing plant species and plant functional group richness. Also, the study of Salamon et al. (2004) showed that total Collembola density and diversity were not significantly affected by plant diversity but the density of certain taxa increased whereas that of others decreased with increasing plant species richness. Similar to Collembola, other belowground biota, such as earthworms, microorganisms, nematodes and mites, have all been shown to respond little to plant diversity (e.g. De Deyn et al. 2004, Ilieva-Makulec et al. 2006, Habekost et al. 2008, Milcu et al. 2008). In contrast to these findings, a recent long-term study on the effects of plant community effects on soil microorganisms of the Jena Experiment field site highlighted the close relationship between plant species richness and soil microbial parameters (Eisenhauer et al. 2010a). This study showed that microorganisms only responded after a time-lag of about four years after establishment of plant diversity manipulations, suggesting that in the long term plant community structure in fact significantly impacts soil microorganisms. This finding supported the relevance of the singular hypothesis of plant species diversity, i.e. the role of individual species, for belowground biota and processes (Eisenhauer et al. 2010a).

Previous experiments investigating plant diversity effects on Collembola were performed one or two years after establishment of experimental treatments (Hedlund et al. 2003, Salamon et al. 2004). This short time span presumably was insufficient to allow for the reduction of soil legacy effects (Bartelt-Ryser et al. 2005, Kulmatiski and Beard 2008, Eisenhauer et al. 2010a). Intimate relationships between plant species richness and soil biota suggest that loss of plant species may not only cause extinction cascades in aboveground communities, but also in those belowground. This needs closer consideration if we are to understand the interrelationships between above- and belowground diversity (Hooper et al. 2000, De Deyn and Van der Putten 2005).

The response of Collembola to increasing plant species and plant functional group richness likely is due to changes in both biotic and abiotic factors. For example, plant diversity affects the diversity and quality of the litter which serves as habitat and food

resource for Collembola (Hopkin 1997). Particularly hemiedaphic species, such as *P. notabilis* and *H. nitidus*, living in upper soil and litter are likely to be influenced by the composition and quality of plant litter materials. Additionally, a more diverse litter layer with more diverse microbial populations may result in increased density and diversity of Collembola (Hågvar 1982). As most species of Collembola at least in part feed on soil microorganisms (Rusek 1998, Chahartaghi et al. 2005), increased microbial biomass (Eisenhauer et al. 2010a) likely contributed to the higher density and diversity of Collembola taxa and life history groups observed in more diverse plant communities.

In addition to consuming microorganisms and litter materials some Collembola species feed on living plant tissue. For example, Protaphorura species feed on fine roots of plants (Ulber 1980, Hurej et al. 1992, Endlweber et al. 2009) and some species of Sminthuridae are primarily phytophagous (Davies 1926, Berg et al. 2004). Therefore, increased plant shoot (Naeem et al. 1994, Spehn et al. 2000, Roscher et al. 2005) and root biomass (Salamon et al. 2004) in more diverse plant communities may increase the availability of food resources for Collembola (Finlay 1985). Moreover, plant diversity has been shown to stabilize Collembola communities via increased quality of root-derived inputs (root litter and exudates; Milcu et al. 2010) which likely contributes to maintaining belowground diversity over time.

EFFECTS OF PLANT FUNCTIONAL GROUP IDENTITY

Plants differ in the quality and quantity of resources that they return to the soil. Hence, plant species are likely to affect decomposer soil biota and the processes that they regulate (Wardle et al. 2004). Previous studies primarily highlighted the significance of the presence of certain plant functional groups for soil biota (Gastine et al. 2003, Hedlund et al. 2003, De Deyn et al. 2004, Salamon et al. 2004, Ilieva-Makulec et al. 2006, Milcu et al. 2008). The design of the present study allowed separating effects of plant species and functional group richness from the effects of plant functional group identity. Supporting our hypothesis (2), plant functional group identity significantly affected Collembola density and diversity. Remarkably, however, impacts of grasses, small herbs and legumes on Collembola were less strong and consistent than effects of plant diversity. While the presence of grasses had significant effects on Collembola density, species richness and Shannon-Wiener diversity index in 0%, 14% and 14% of the cases, respectively, the presence of small herbs had significant effects in 10%, 57% and 29% of the cases, respectively (Tables 2.2-2.4).

Moreover, legumes which are regarded as one key plant functional group in grassland systems (Milcu et al. 2008) significantly affected Collembola density, species richness and Shannon-Wiener diversity index in only 10%, 29% and 14% of the cases, respectively. By contrast and as highlighted above, plant species richness strongly impacted Collembola density, species richness and Shannon-Wiener diversity index, namely in 70%, 86% and 43% of the cases.

The mechanisms responsible for the impacts of plant functional group identity are manifold and vary with plant functional group, Collembola life history group and season. In contrast to previous studies on the role of small herbs for belowground biota and ecosystem functioning, we found them to strongly affect Collembola. Generally, the effect of small herbs on Collembola density and diversity was negative but the effect differed between seasons. The density of Hypogastruridae, total Collembola species richness (particularly that of euedaphic and hemi- to epedaphic species) and the Shannon-Wiener diversity index of euedaphic and hemi- to epedaphic species decreased in the presence small herbs, while the density of hemiedaphic species and the diversity of Isotomidae increased in spring but decreased in autumn. Negative effects of small herbs were likely due to low plant productivity (Marquard et al. 2009) and thus food availability as is the case in other soil biota (Spehn et al. 2000, Gastine et al. 2003, Salamon et al. 2004). However, small herbs also beneficially affected certain Collembola taxa in spring. This might have been due to more benign micro- climate underneath creeping shoots and rosettes (Roscher et al. 2004). However, the soil core samplings were performed in varying time lags after the first (after circa 2 weeks) and second mowing (after circa 10 weeks) of the aboveground plant material which might have also affected the availability of resources for Collembola and the differences between seasons.

Beneficial effects of grasses on Collembola as found in the present study have been reported previously (Salamon et al. 2004, Milcu et al. 2006). Grasses are characterized by a pronounced root system which contributes to the build-up of high microbial biomass (Carpenter-Boggs et al. 2003, Eisenhauer et al. 2010a). Since Collembola in part feed on plant root associated microorganisms (Bardgett et al. 1993b, Rusek 1998) the rhizosphere of grasses is likely to improve food availability. In contrast to grasses, the fine root system of small herbs is less pronounced in the Jena Experiment (Bessler et al. 2009) and therefore probably provides less food resources for Collembola, particularly for euedaphic species, resulting in low Collembola density and diversity in autumn.

Legumes are considered key plant species (Mulder et al. 2002, Spehn et al. 2002, Scherber et al. 2006, Milcu et al. 2008) strongly affecting soil invertebrates by providing

nitrogen-rich litter material (Spehn et al. 2002) and increasing microbial biomass (Denton et al. 1999). Thus, both the quantity and quality of plant residues might have been increased in the presence of legumes (Roscher et al. 2008, Marquard et al. 2009). Unexpectedly and in contrast to previous studies (Salamon et al. 2004), legumes had little effect on Collembola in the present study. Consistent with these findings, the importance of legumes for soil microorganisms decreased in time (Eisenhauer et al. 2010a) which was likely due to poorly developed root systems (Eisenhauer and Scheu 2008, Bessler et al. 2009). Milcu et al. (2006) found Collembola density even to be detrimentally affected by legumes in a laboratory experiment.

2.6 CONCLUSIONS

The present study shows that four years after the establishment of experimental plant communities Collembola density and diversity significantly increased with plant species richness, highlighting the singular hypothesis of plant species diversity for soil biota. Moreover, plant community impacts largely were consistent early and late in the seasons suggesting generality of our results. We propose an intimate relationship between plant species richness and the performance and diversity of soil biota in the long term, questioning the adequacy of conclusions derived from previous short-term experiments. Since soil animals, such as Collembola (Eisenhauer et al. 2010c), essentially contribute to the functioning of terrestrial ecosystems, we suggest that only long-term studies considering delayed soil feedbacks may display the realistic scenarios of how biodiversity affects ecosystem functions.

Chapter 3

Collembola Species Composition and Diversity Effects on Ecosystem Functioning Vary with Plant Functional Group Identity

3.1 ABSTRACT

The relationship between decomposer diversity and ecosystem functioning is little understood although soils accommodate a significant proportion of worldwide biodiversity. Collembola are among the most abundant and diverse decomposers and are known to modify plant growth. We examined the effects of Collembola species diversity (one, two and three species belonging to different life history groups) and composition on litter decomposition and the performance of plant communities (above- and belowground productivity) of different functional groups (grasses, herbs and legumes).

Collembola densities did not increase with diversity indicating niche overlap. Generally, Collembola species composition was a better predictor for ecosystem functioning than Collembola species number with the impacts of Collembola diversity and composition on ecosystem functioning strongly depending on plant functional group identity. Non-linear effects of Collembola diversity on litter decomposition and plant productivity suggest pronounced and context dependent species interactions and feeding habits. Net surface litter decomposition was decreased by Collembola, whereas root litter decomposition was at maximum in the highest Collembola diversity treatment. Herbs benefitted most from the presence of three Collembola species. Similarly, Collembola diversity influenced root depth distribution in a plant functional group specific way: while grass root biomass decreased with increasing Collembola diversity in the upper and lower soil layer, legume root biomass increased particularly in the lower soil layer.

Idiosyncratic and context dependent effects of Collembola diversity and composition even in rather simple assemblages of one to three species suggest that changes in Collembola diversity may have unpredictable consequences for ecosystem functioning. The finding that changes in Collembola performance did not directly translate to alterations in ecosystem functioning indicates that response traits do not necessarily conform to effect traits. Distinct plant functional group specific impacts of Collembola diversity on root depth distribution are likely to modify plant competition in complex plant communities and add a novel mechanism how decomposers may affect plant community assembly.

3.2 INTRODUCTION

The progressive simplification of ecosystems worldwide has generated concern about the consequences for ecosystem functions and services (Sala et al. 2000, Millennium Ecosystem Assessment 2005). This prompted a multitude of biodiversity experiments in the last two decades; however, the importance of belowground diversity for ecosystem functioning has received comparatively little attention and continuous to be debated (Bradford et al. 2002, Bardgett and Wardle 2010). This is surprising since decomposers drive essential ecosystem functions, such as organic matter turnover and nutrient cycling, thereby functioning as key determinants of soil fertility and nutrient uptake by plants (Bradford et al. 2002, Coleman et al. 2004, Wardle et al. 2004, Bardgett and Wardle 2010). Moreover, soils accommodate a significant proportion of the worldwide biodiversity (at least 25% of described living species; Bardgett and Wardle 2010, Decaëns 2010). Nevertheless, studies on belowground communities and their impact on ecosystem properties form a relatively new field in ecology and thus the functional diversity of soil organisms and its implications are still largely unexplored (Wolters 2001, Bardgett et al. 2005).

There is evidence that decomposer diversity is crucial for decomposition processes and plant N availability (Bardgett and Cook 1998, Bardgett and Shine 1999, Mikola et al. 2002, Heemsbergen et al. 2004, Tiunov and Scheu 2005a), although effects may be more pronounced at the lower end of the diversity gradient (Laakso and Setälä 1999, Cragg and Bardgett 2001). Heemsbergen et al. (2004) highlighted the importance of interspecific functional dissimilarity in decomposer diversity effects on soil processes. Similarly, Eisenhauer et al. (2010b) showed that functionally dissimilar decomposer groups can synergistically impact plant and herbivore performance. However, little is known about diversity effects of decomposer species of similar size and life history strategies. Previous studies reported considerable functional redundancy at the species scale (Laakso and Setälä 1999, Wardle 1999) and suggested that soil processes are mainly driven by physiological attributes of the dominant decomposer species (Laakso and Setälä 1999, Cragg and Bardgett 2001). However, Wolters (2001) proposed that the number of soil animal species needed to maintain ecosystem functioning may depend on the number of functions investigated.

To gain further insight into decomposer species diversity effects on ecosystem functioning, we conducted a microcosm greenhouse experiment investigating the response of soil surface litter decomposition and above- and belowground productivity of three different

plant communities (grasses, herbs and legumes) to variations in the number and composition of Collembola species differing in life history traits.

Collembola are among the most abundant microarthropods in soil (Bardgett et al. 1993c, Hopkin 1997) with densities of up to 60,000 ind./m^2 in grasslands (Gange and Bower 1997). Feeding predominantly on fungi (Hopkin 1997, Rusek, 1998), they mobilize nutrients locked up in microbial biomass, thereby affecting plant nutrition (Harris and Boerner 1990, Lussenhop 1992, Wardle 1999). Depending on Collembola density, growth and respiration of microorganisms are either stimulated or reduced (Theenhaus et al. 1999, Cole et al. 2004). In addition to microorganisms, Collembola also feed on dead organic matter as well as living plant tissue and fine roots (Hurej et al. 1992, Chahartaghi et al. 2005, Endlweber et al. 2009). Previous greenhouse experiments showed mainly positive effects of Collembola on plant biomass production, however, effects varied with Collembola density, plant functional group and plant species identity (Scheu et al. 1999, Kreuzer et al. 2004, Partsch et al. 2006). Particularly non-legume herbs were shown to benefit from Collembola presence (Partsch et al. 2006, Eisenhauer et al. 2010c). Only few studies investigated the impacts of Collembola diversity on plant performance (Cragg and Bardgett 2001, Cole et al. 2004). These studies suggest that effects of two- and three-species combinations of Collembola are due to identity effects of Collembola species, rather than to the number of species per se (Cragg and Bardgett 2001). Furthermore, they indicate that changes in the diversity of Collembola may affect soil processes in an idiosyncratic way (Cragg and Bardgett 2001). However, interspecific interactions between Collembola species, such as competition and facilitation, may affect ecosystem functioning. For instance, it is known that competition between Collembola species drives their vertical distribution in soil (Klironomos and Kendrick 1996). Furthermore, the impact of Collembola species on soil processes may vary with soil depth, and Collembola species are known to predominantly colonize certain soil layers (Faber and Verhoef 1991, Berg and Bengtsson 2007). Likewise, complementary interactions among decomposer species such as facilitation have been shown to be important drivers of ecosystem processes (Heemsbergen et al. 2004), which might also apply to Collembola species.

Therefore, not only presence of certain Collembola species but also species diversity of Collembola may be important for litter decomposition and plant productivity. We hypothesized that (1) Collembola density, litter decomposition and plant productivity increases with increasing Collembola diversity due to complementary interactions among

Collembola species, and (2) Collembola diversity effects depend on plant functional group identity due to varying nutrient requirements.

3.3 MATERIALS AND METHODS

EXPERIMENTAL SETUP

The experiment was conducted in a temperature-controlled greenhouse (18°C; 70% humidity; 16 h illumination, photosynthetically active photon flux density > 250 µMol m^{-2} s^{-1}) and set up in microcosms consisting of PVC tubes (inner diameter 10 cm, height 20 cm), which were sealed at the bottom by 1 mm mesh (Fig. 3.1B). The tubes were prolonged at the top by a plastic barrier (10 cm height) to prevent Collembola from escaping. The microcosms were filled to a height of 15 cm with 1.5 kg (fresh weight) of sieved (2 mm) and homogenized soil (equivalent to 1.25 kg dry weight). The soil (pH 8.1, nitrogen content 0.3%, carbon content 4.6%, C/N ratio 15.7) was taken from the south-eastern edge of the Jena Experiment field site, a large grassland biodiversity experiment in Germany (Roscher et al. 2004), and defaunated by freezing at -22°C for two weeks (Huhta et al. 1989). To track nutrient assimilation by the plants, 1.25 g of ^{15}N labelled *Lolium perenne* L. root litter material (30 atom% ^{15}N) was cut into pieces < 0.5 mm and homogeneously mixed into the soil of the microcosms. To leach nutrients from the soil which became available during the defaunation process, microcosms were irrigated with 50 ml deionized water per day for 6 days prior to the start of the experiment.

Nine plant species belonging to three plant functional groups (grasses, herbs and legumes) were selected from the species pool of the Jena Experiment and grown to a height of approx. 5 cm (for three weeks) from seeds in pots filled with defaunated Jena soil in the greenhouse. Legume seeds were mechanically scarificated to stimulate germination. The seeds were purchased from Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany. Four seedlings of each grass (*Lolium perenne* L., *Dactylis glomerata* L., *Phleum pratense* L.), herb (*Knautia arvensis* L., *Crepis biennis* L., *Centaurea jacea* L.) and legume species (*Trifolium repens* L., *Trifolium pratense* L., *Medicago varia* L.) were transplanted into the microcosms to establish three different plant functional group communities (grasses, herbs and legumes), each consisting of twelve plant individuals of every plant functional group (Fig. 3.1C). After transplanting the seedlings, the microcosms were watered every second day

with 50 ml portions of deionized water to ensure successful establishment of the plants; germinating weeds were removed after establishment of microcosms over a period of 14 days. Subsequently, 20 medium-sized adult individuals of each *Folsomia candida* (Willem, 1902), *Heteromurus nitidus* (Templeton, 1835) and *Protaphorura armata* (Tullberg, 1869) from laboratory cultures were added to the microcosms to establish the following Collembola treatments: (1) control treatment without Collembola, (2) single-species treatments for each of the three species (monocultures), (3) two-species treatments comprising every possible two-species combination (three), and (4) three-species treatment comprising each of the three Collembola species (Fig. 3.1A). In the following we will use the genus names for the different Collembola species. These Collembola species belong to three different life history groups: *Folsomia* is epedaphic, *Heteromurus* is hemiedaphic and *Protaphorura* is euedaphic (Gisin, 1943). Each treatment was replicated four times giving a total of 96 microcosms which were placed in the greenhouse and randomized every week to avoid edge effects.

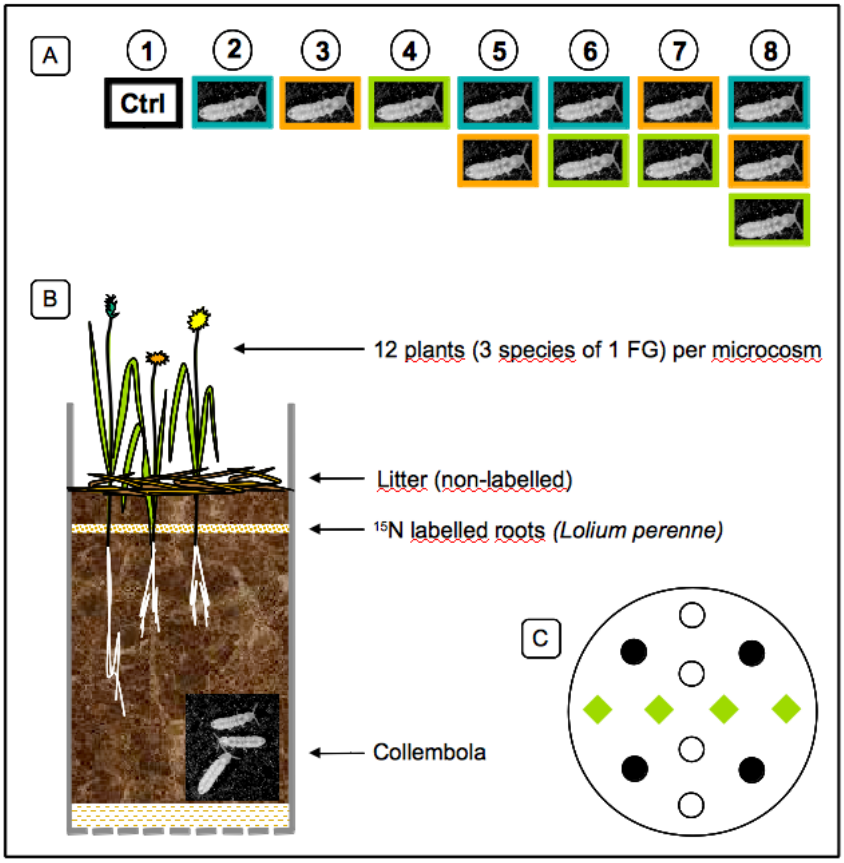

Figure 3.1 Scheme of the experimental setup. (**A**) Collembola treatments comprising every possible species combination, as well as the control treatment [Ctrl]. (**B**) Cross section of one microcosm illustrating the various components of the experiment. (**C**) Scheme demonstrating the pattern in which the plants were arranged in each microcosm.

To simulate conditions in the field, provide initial surface cover and investigate litter decomposition, 3 g of dried litter material were placed on top of the soil after Collembola addition. The litter material (2.53% N, C/N ratio 17.3, dried at 60°C, cut into 3 cm pieces) was collected near the study site and consisted mainly of grass and herb leaves (Fig. 3.1B). Microcosms were irrigated daily with an increasing quantity of deionized water (initially 50 ml every two days, after 10 weeks up to 150 ml per day) according to the requirements of the growing plants in order to avoid water limitation. All microcosms received the same amount of water to avoid effects of different watering.

HARVEST AND MEASUREMENTS

After 15 weeks plant shoots were harvested by cutting them at soil surface level, separated to species, dried at 60°C for 5 days and weighed. Soil cores were removed from the microcosms and separated into three layers (0 - 5 cm, 5 - 10 cm, 10 - 15 cm depth), and Collembola were extracted by heat from each of the layers (Kempson et al. 1963). Collembola were collected in glycerol, transferred into 70% ethanol and species were identified and counted. Roots were washed out of the soil of each layer using a 1 mm mesh, dried at 60°C for 5 days and weighed; it was not possible to separate roots of single plant species. For ^{15}N analysis, selected shoots were ground to powder, weighed into tin capsules (approx. 1 mg), and total N content and ^{15}N signatures were measured by an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) coupled with a gas isotope mass spectrometer (MAT 251, Finnigan, Bremen, Germany) (Reineking et al. 1993). Atmospheric N_2 served as basis for $\delta^{15}N$ calculation and acetanilide (C_8H_9NO, Merck, Darmstadt, Germany) as internal standard. The litter material which remained on the soil surface was sampled, dried (60°C, 5 days) and weighed. We calculated net decomposition, net shoot and root productivity by relating the respective treatments with the presence of Collembola to control treatments without Collembola per plant functional group [%].

STATISTICAL ANALYSIS

Prior to statistical analysis, data on Collembola numbers and plant biomass were log-transformed ($\log_{10}[x + 1]$), if necessary, to meet the requirements of analysis of variance (ANOVA; normal distribution and homoscedasticity of error variances). Means presented in the text and figures were calculated using non-transformed data (± standard error). Comparisons of means were performed using Tukey's HSD test ($\alpha = 0.05$).

In order to explore the effects of Collembola diversity on response variables we used two different statistical models. First, the effects of plant functional group identity (PFG; grasses, herbs and legumes), Collembola diversity (CD; 1, 2 and 3 species), presence of the Collembola species *Folsomia* (FOL), *Heteromurus* (HET), and *Protaphorura* (PRO) and interactions between PFG and Collembola species on total Collembola density, net decomposition, net shoot productivity and net root productivity were analyzed sequentially using ANOVA as part of the general linear model (GLM, type I sum of squares; Model A). PFG was always fitted first, followed by CD, the interaction between these two factors, FOL, HET, PRO (whose sequence was alternated in separate analyses), ant the interactions between PFG and the presence of certain Collembola species (whose sequence was alternated in separate analyses). F-values given in text and tables refer to those where the respective factor and interaction was fitted first (Schmid et al. 2002). Second, the effect of PFG and Collembola community composition (CC; FOL, HET, PRO, FOL & HET, FOL & PRO, HET & PRO, FOL & HET & PRO) on the variables mentioned above were analyzed using ANOVA (type III sum of squares; Model B). Additional repeated measures ANOVA was performed to test the effects of PFG, CD (or CC) and soil depth (0 - 5, 5 - 10 and 10 - 15 cm) on root biomass. Similarly, repeated measures ANOVA was performed to analyze the effects of PFG, CD (or CC) and soil depth (0 – 5 and 5 - 10 cm; 10 - 15 cm was not included in the analysis due to very low numbers) on the relative density of Collembola in the deeper soil layer. Finally, ANOVA was used to investigate the effects of Collembola (COL; control treatment without Collembola, presence of Heteromurus, and presence of all three Collembola species) on ^{15}N signatures in herb shoot tissue in order to investigate if observed effects of Heteromurus on herb shoot and root biomass were due to elevated belowground N mineralization. This subset was chosen due to pronounced treatment impacts on the productivity of grasses and herbs. All statistical analyses were performed using STATISTICA 7 (Statsoft).

3.4 RESULTS

COLLEMBOLA DENSITY

On average, 1,678 Collembola were found in each microcosm at the end of the experiment. Collembola density at the start of the experiment was not related to final Collembola density ($R^2 < 0.01$, $P = 0.75$), indicating that Collembola diversity effects were not due to initial differences. Collembola densities differed significantly between plant functional groups, being significantly higher in grass (2,109 ± 218 individuals microcosm^{-1}) and herb communities (1,823 ± 239 individuals microcosm^{-1}) than in legume communities (1,102 ± 223 individuals microcosm^{-1}; Table 3.1, Fig. 3.2A). Collembola densities were significantly lower in treatments containing *Heteromurus* than in those without this species (-31%; Table 3.1). However, Collembola densities depended also on interactions between single species as indicated by a significant effect of Collembola composition and a higher proportion of explained variance by Model B (Table 3.1, Fig. 3.2A). On average, 22% of total Collembola were found in the second soil layer (5 - 10 cm). The depth distribution of Collembola depended on plant functional group identity and Collembola diversity. Significantly more Collembola were found in the deeper soil layer of legume communities than in that of grass communities (+10%; $F_{2,75} = 4.33$, $P = 0.017$). Moreover, a higher proportion of Collembola was found in the deeper soil layer of treatments containing two Collembola species than in monocultures of Collembola (+8%; $F_{2,75} = 3.91$, $P = 0.024$).

LITTER DECOMPOSITION

Overall, net decomposition was 88% (2.01 g decomposed). It was significantly lower in legume communities than in grass communities (Table 3.1, Fig. 3.2B). However, the effect of plant functional group identity depended on the presence of Folsomia as well as on the presence of Protaphorura (Table 3.1, Fig. 3.2B), as indicated by the significant interaction between plant functional group identity and each of these Collembola species (Table 3.1). Net litter decomposition was increased in the presence of Folsomia in grass (+8%) and herb communities (+12%), whereas it was decreased in legume communities (-12%; Table 3.1). Moreover, net litter decomposition was lower in grass communities in the presence of Protaphorura (-17%), little affected in herb communities (-1%) and increased in legume communities (+8%; Table 3.1). Again, Model B explained considerably more variance than

Model A, suggesting distinct interactions between Collembola species in litter decomposition (Table 3.1, Fig. 3.2B).

Table 3.1 ANOVA-table of F- and P-values for the effects of plant functional group (PFG; grass, herb, legume), Collembola diversity (CD; 1, 2, 3), presence of *Folsomia candida* (FOL; 0, 1), *Heteromurus nitidus* (HET; 0, 1) and *Protaphorura armata* (PRO; 0, 1) on Collembola density [individuals per pot], net decomposition (as compared to control treatments without Collembola; [%]), net shoot and net root productivity (both [%]) (Model A). ANOVA-table of F- and P-values for the effects of PFG and Collembola community composition (CC; three monocultures, all possible two-species mixtures and three-species mixture) on Collembola density, net decomposition, net soot and net root productivity (Model B).

		Collembola density		Net decomposition		Net shoot productivity		Net root productivity	
	D.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Model A (R^2)		0.37		0.39		0.36		*0.53*	
PFG	2	7.20	0.0014	10.45	0.0001	1.43	0.2471	12.65	<.0001
CD	2	2.19	0.1193	2.70	0.0746	3.17	0.0483	5.92	0.0042
PFG x CD	4	1.50	0.2126	0.63	0.6455	2.72	0.0364	5.35	0.0008
FOL	1	3.47	0.0668	3.55	0.0637	4.59	0.0356	2.65	0.1079
HET	1	9.46	0.0030	3.40	0.0694	2.41	0.1254	5.16	0.0263
PRO	1	1.47	0.2293	0.00	0.9681	0.35	0.5558	0.41	0.5231
PFG x FOL	2	1.53	0.2242	3.96	0.0236	5.54	0.0058	5.97	0.0041
PFG x HET	2	0.99	0.3784	1.03	0.3633	4.42	0.0157	2.32	0.1059
PFG x PRO	2	2.06	0.1356	3.46	0.0371	0.21	0.8145	2.40	0.0984
Error	69								
Model B (R^2)		*0.43*		*0.47*		*0.41*		*0.54*	
PFG	2	7.21	0.0015	10.82	<.0001	1.88	0.0990	11.70	<.0001
CC	6	2.43	0.0352	1.97	0.0838	1.41	0.1519	2.71	0.0210
PFG x CC	12	1.47	0.1611	1.78	0.0711	2.43	0.0116	2.80	0.0040
Error	63								

D.f. = Degrees of freedom; Significant effects are given in bold; the model explaining more variance is given in italics.

PLANT PRODUCTIVITY

Overall, legumes (22.84 ± 0.52 g) built significantly more biomass than grass (3.50 ± 0.08 g) and herb communities (3.09 ± 0.14 g; $F_{2,69} = 1371.93$, $P < 0.0001$), whereas net plant shoot productivity did not differ between plant functional groups (Table 3.1, Fig. 3.2C). However, net shoot productivity depended on the interaction between plant functional group identity and Collembola diversity and Collembola composition, respectively (Table 3.1, Fig. 3.2C). Net shoot productivity was significantly higher in herb communities containing three Collembola species than in those containing two Collembola species (Fig. 3.2C). Moreover, the presence of *Heteromurus* increased net shoot productivity of herbs, except in the two-species mixture with *Folsomia* (Fig. 3.2C). This resulted in a significant interaction between plant functional group identity and the presence of *Heteromurus* (Table 3.1): net shoot productivity of grasses (-3%) and legumes (-1%) was little affected by the presence of *Heteromurus*, whereas that of herb communities was increased considerably (+25%; Fig. 3.2C) decreased. Moreover, while net shoot productivity was not affected by the presence of *Folsomia* in grass and legume communities, it was lower in herb communities (-20%; Table 3.1). The dependency of *Heteromurus* effects on other Collembola species and a higher explanatory value of Model B highlight the complex interactions between Collembola species in affecting plant productivity (Table 3.1).

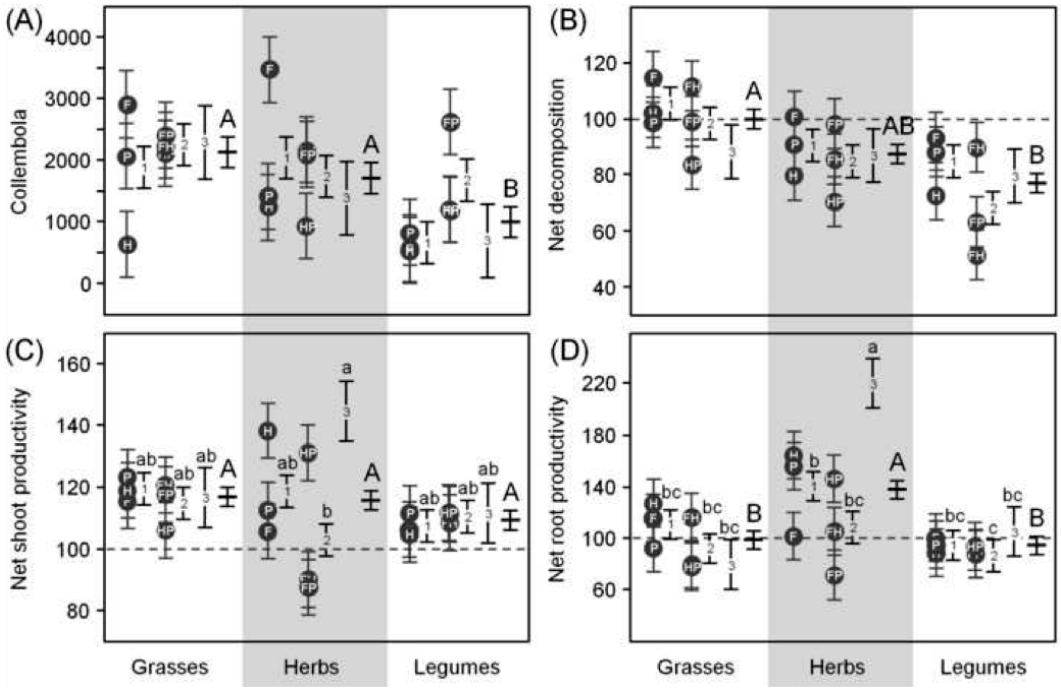

Figure 3.2 Effects of plant functional group identity (grasses, herbs and legumes) and Collembola diversity (1, 2 and 3 species) or plant functional group identity and Collembola species composition (F = *Folsomia candida*, H = *Heteromurus nitidus*, P = *Protaphorura armata*) on (**A**) the density of Collembola per microcosm, (**B**) net decomposition ([% of initial]; in relation to treatments without Collembola), (**C**) net shoot productivity [g per microcosm], (**D**) net root productivity [g per microcosm]. Bars with different letters vary significantly (Tukey's HSD test, $\alpha = 0.05$). Capital letters indicate differences between plant functional groups; lowercase letters indicate variations of Collembola diversity effects in the presence of different plant functional groups. Means with standard error. For facility of inspection herb communities are highlighted with grey background and Tukey's HSDs are only given for significant interactions between plant functional group identity and Collembola diversity.

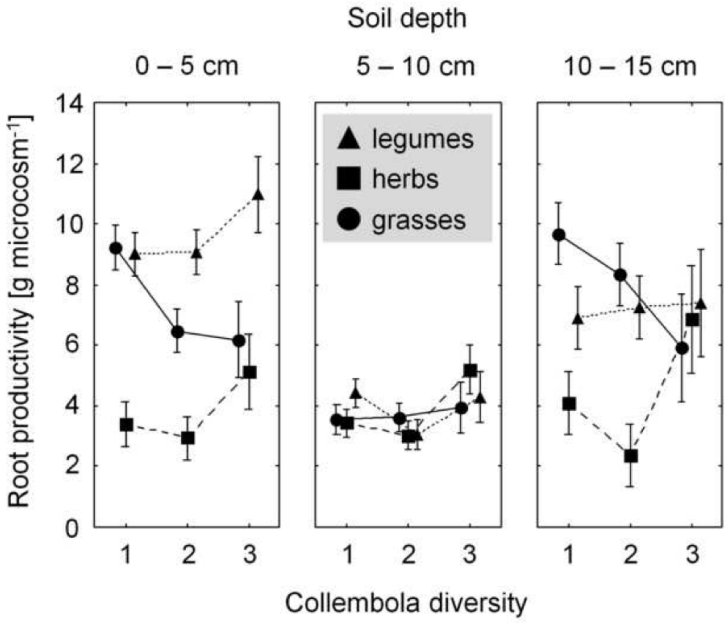

Figure 3.3 Effects of plant functional group identity (grasses, herbs and legumes), Collembola diversity (1, 2 and 3 species) and soil depth (0 – 5, 5 – 10 and 10 – 15 cm) on root productivity [g per microcosm]. Means with standard error.

On average, grass (19.85 ± 1.39 g) and legume communities (20.44 ± 0.72 g) built significantly more root biomass than herb communities (10.35 ± 0.87 g; $F_{2,69} = 41.24$, $P < 0.0001$). Net root biomass productivity was significantly higher in herb communities than in grass and legume communities (Table 3.1, Fig. 3.2D). Similar to net shoot productivity, net root productivity was significantly affected by the interactions between plant functional group identity and Collembola diversity and Collembola composition, respectively (Table 3.1, Fig. 3.2D). Again, herb communities benefited in particular from the presence of *Heteromurus* (+18%; Table 3.1, Fig. 3.2D). Moreover, net root productivity was significantly higher in herb communities containing three Collembola species than in all other treatments. In addition, net root productivity was significantly higher in herb communities containing one Collembola species than in legume communities containing two Collembola species (Fig. 3.2D). The impact of Folsomia presence depended on plant functional group identity with little effects on net root productivity of grass (-2%) and legume communities (+3%), but a distinct decrease on that of herb communities (-31%; Table 3.1). Model A and B explained the same proportion

of variance (Table 3.1) indicating that Collembola diversity and presence of single taxa were good predictors of net root productivity. This was also true for root depth distribution which is why only results of Model A are shown in the following. Root biomass was significantly affected by an interaction between plant functional group identity, Collembola diversity and soil depth ($F_{8,146} = 2.34$, $P < 0.021$). While root biomass increased with increasing Collembola diversity in legume and herb communities in the upper soil layer, it decreased in grass communities (Fig. 3.3). Collembola diversity showed little effects in the intermediate soil layer, whereas root biomass of grasses decreased with increasing Collembola diversity and that of herbs increased from two to three species mixtures (Fig. 3.3).

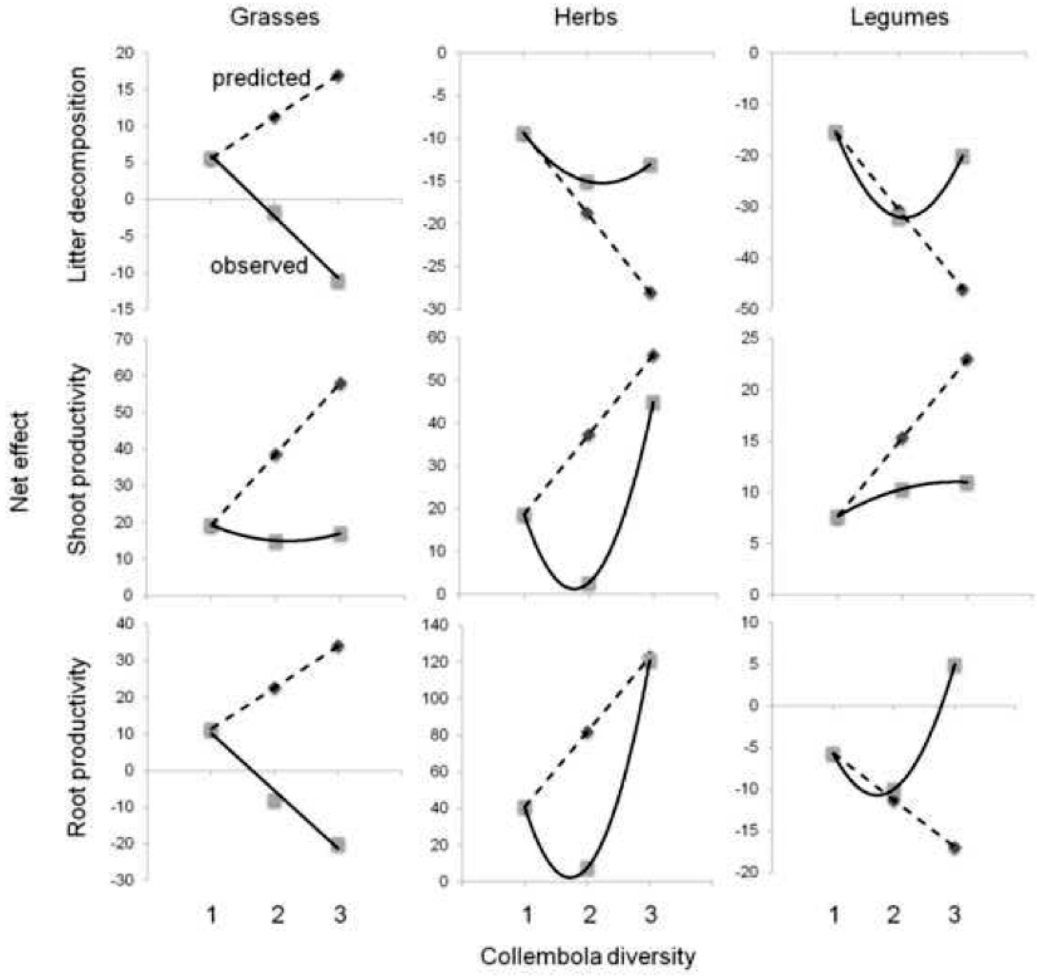

Figure 3.4 Qualitative comparison between predicted net effects of Collembola diversity (1, 2 and 3 species) based on an additive model (diamonds, dashed line) and observed effects in mixtures (squares, solid line). Litter decomposition is given in the first row; grass communities are given in the first column, herb communities in the second and legume communities in the third column.

^{15}N SIGNATURES IN HERB SHOOT TISSUE

The $\delta^{15}N$ value in shoots of herbs was significantly higher (176 ± 11; +21%) than in shoots of grasses (141 ± 9; $F_{1,54} = 7.43$, $P = 0.0086$) but did not differ significantly between single species of each plant functional group ($F_{4,54} = 0.44$, $P = 0.78$). Irrespective of plant functional group and plant species identity, presence of all three Collembola species significantly increased ^{15}N values in plant shoot tissue by +39% and +47% as compared to the control and *Heteromurus* treatments, respectively ($F_{2,54} = 8.32$, $P = 0.0007$).

3.5 DISCUSSION

Results of the present experiment show that Collembola species composition is a better predictor for ecosystem functioning than Collembola species number. Litter decomposition and plant productivity resulted from non-linear effects of Collembola diversity. Ecosystem functioning was not only driven by certain Collembola species but by pronounced species interactions as indicated by non-additive effects of species mixtures (Fig. 3.4). Moreover, our results show that impacts of Collembola diversity and composition on litter decomposition and plant productivity strongly depend on plant functional group identity. Distinct plant functional group specific impacts of Collembola diversity on root depth distribution are likely to modify plant competition in complex plant communities. Changes in Collembola performance did not directly translate to alterations in ecosystem functioning suggesting that Collembola response traits do not necessarily conform to effect traits.

COLLEMBOLA PERFORMANCE

We hypothesized that Collembola performance varies with Collembola diversity due to complementary interactions and between plant communities of different functional groups due to differences in the quantity or quality of plant derived inputs. In contrast to our expectations, Collembola densities depended on community composition and not on diversity. Particularly communities containing *Heteromurus* had significantly lower densities, whereas communities with *Folsomia* tended to have higher densities. The missing diversity effect on Collembola performance points to distinct niche overlaps between the species although they belong to varying life history groups (Gisin 1943). Thus, we assume that interspecific competition for food and living space hampered Collembola performance. This is supported

by the finding that a significantly higher proportion of Collembola was found in the deeper soil layer in two species mixtures than in monocultures. Similarly, Klironomos and Kendrick (1996) reported that even Collembola species preferentially colonizing the litter layer were forced into deeper soil layers in presence of competitors. Cragg and Bardgett (2001) found that interspecific competition within experimental microcosms promoted the suppression or elimination of one or more of the competing species in favor of the dominant one, thereby changing dominance structure. However, this was not the case in our experiment. Presumably, inferior species avoided competitive exclusion by switching diet thereby increasing resource partitioning (Jørgensen et al. 2003). This hypothesis is supported by assumptions of Cortet et al. (2003) that Collembola are able to adapt their diet and choose alternative food resources if competition becomes more severe.

In accordance with our expectations, Collembola performance varied between plant functional groups. Collembola density was significantly lower in legume than in herb and grass communities. This is in line with results from previous greenhouse experiments in which Collembola density was highest in grass and lowest in legume systems (Milcu et al. 2006, Endlweber and Scheu 2007). However, results of our study do not support the conclusion drawn in these studies that Collembola benefit from high root biomass of grasses, as in our experiment root biomass in legume and grass systems was similar. Moreover, Collembola density was not correlated with root biomass ($R^2 < 0.01$, $P = 0.66$). Rather, the results suggest that high biomass production of legumes, which exceeded that of grasses and herbs by more than a factor of six, depleted nutrients in soil and thereby reduced fungal growth, i.e. the amount of food resources available for Collembola. Another explanation for the negative legume effect could be that legumes decreased soil water content by transpiring more than grass and herb communities. Although we lack data on soil water content, this assumption is supported by a negative correlation between plant shoot biomass and Collembola density ($R^2 = 0.11$, $P = 0.0024$).

LITTER DECOMPOSITION

Litter decomposition was decreased by Collembola supporting the findings of a recent meta-analysis of >100 litter bag experiments (Kampichler and Bruckner 2009). Although Kampichler and Bruckner (2009) found a slightly positive effect of microarthropods on decomposition, this relationship was reversed to a negative one when they corrected for the effect of mesh size. Remarkably, decreased decomposition occurred only in herb and legume

communities in the present experiment, suggesting that Collembola feeding behavior and thus effects on ecosystem functioning are context dependent and Collembola species specific. Collembola appear to be generalist feeders using a great diversity of resources (Rusek 1998, Ponge 2000, Endlweber et al. 2009), and our results suggest that although Collembola preferentially fed on saprotrophic fungi rather than surface litter material, thereby decreasing its decomposition rate, the different species may have switched diets in response to other species present and to plant functional group identity. This assumption is supported by the niche overlaps between the Collembola species mentioned above. The dependence of Collembola identity effects on plant functional group identity and a marginally significant interaction between plant functional identity and Collembola community composition indicate that feedings habits are remarkably plastic and complex interactions between single Collembola species and their environment have to be considered to predict litter decomposition. This is in line with findings of Cragg and Bardgett (2001) suggesting that effects of soil fauna on litter decomposition processes are strongly influenced by the composition of the decomposer community. Thus, the present results of neutral to negative effects of Collembola diversity on soil surface litter decomposition contradict our hypothesis (1), but confirm hypothesis (2) as impacts depended on the plant community. Remarkably, ^{15}N signatures in grass and herb shoots were increased in three-species treatments as compared to the control and Heteromurus only treatments, indicating that high Collembola diversity promoted plant assimilation of soil derived nitrogen by enhancing decomposition of root litter.

PLANT PRODUCTIVITY

Plant biomass production essentially relies on the availability of nutrients provided by the decomposer community. Collembola have been shown to affect plant productivity either directly by feeding on plant roots and other living plant tissue (Hurej et al. 1992, Rusek 1998, Endlweber et al. 2009) or indirectly by altering plant nutrient supply either via changing microbial activity or via nutrient excretion (Bardgett et al. 1993c, Cole et al. 2004, Partsch et al. 2006). Overall, net shoot and root productivity was increased in the presence of Collembola in the present study; however, this depended strongly on the interaction between Collembola diversity, community composition and plant functional group identity. Shoot and root productivity was at a maximum in the highest Collembola diversity level in herb communities suggesting a non-linear and context dependent impact of Collembola diversity.

Thus, hypothesis (1) is only confirmed in part, whereas effects depended on plant functional group identity confirming hypothesis (2). These results correspond to the findings of Endlweber and Scheu (2007) who concluded that effects of Collembola on plant productivity depend on plant species. The lack of Collembola effects on legume biomass production in our experiment might have been due to a considerable depletion of nutrients in soil and low soil water content as a result of high biomass production in legume communities, resulting in reduced fungal biomass and/or Collembola density. Moreover, the fact that legume productivity remained unaffected by Collembola diversity is conform to the findings of Kreuzer et al. (2004) and Endlweber and Scheu (2007) and confirms that legumes due to N-fixing are little responsive to changes in soil nutrients and therefore to decomposer invertebrates (but see Eisenhauer and Scheu 2008).

Net herb shoot and root productivity were at a minimum in two species mixtures and at maximum in three species mixtures. This pattern is difficult to explain but might have been due to the movement of Collembola to deeper soil layers in two species mixtures. Collembola not only feed on dead organic matter and soil microorganisms; several species also consume living plant tissue and directly graze on plant fine roots (Hurej et al. 1992, Endlweber et al. 2009). Increased Collembola density in deeper soil layers associated with diet switching (Cortet et al. 2003, Jørgensen et al. 2003) might have led to increased feeding on fine roots (Endlweber and Scheu 2007), thereby reducing uptake of nutrients by the plants in two Collembola species mixtures (Murray et al. 2002, Newingham et al. 2007). Supporting this assumption, high densities of Collembola, as in the present study, have been shown to detrimentally affect plant growth (Harris and Boerner 1990, Cole et al. 2004).

Lower plant productivity in two species mixtures and negative net effects of certain Collembola mixtures suggest that Collembola may either inhibit or facilitate plant growth. Reduced plant performance in two species treatments mainly was due to Collembola mixtures comprising *Folsomia* and *Protaphorura*. This is in line with results from Heemsbergen et al. (2004) who found that changes in soil processes are mainly due to differences in species composition rather than species numbers. *Folsomia* and *Protaphorura* are similar in size and body shape and both feed on a variety of food resources including organic matter, fungi and small litter fragments (Hopkin 1997). This might have led to increased interspecific competition for food resources and low decomposition of large litter fragments and therefore low nutrient mineralization. In fact, litter mass loss was lowest in two species treatments. In three species mixtures the larger species *Heteromurus* likely facilitated resource acquisition

by *Folsomia* and *Protaphorura* by comminution of large root litter fragments, thereby increasing resource availability for the smaller Collembola species. Indeed, ^{15}N signatures in shoot tissue were highest in three species mixtures indicating elevated root litter decomposition. Facilitative interactions between different species have been shown to increase resource consumption (Cardinale et al. 2002), which in turn may lead to increased nutrient mineralization and plant growth. These results accord to the findings of Heemsbergen et al. (2004) and Eisenhauer et al. (2010b) who concluded that species mixtures containing functionally more dissimilar species may result in facilitative interactions and better performance than mixtures with functionally more similar species.

The response of plant productivity to Collembola diversity and composition varied with plant functional groups, which is consistent with the findings of Partsch et al. (2006) and Eisenhauer et al. (2010c) who reported most pronounced Collembola effects on herbs. While legume communities were unresponsive, root biomass of grasses decreased significantly with increasing Collembola species numbers. As discussed earlier, this likely resulted from increased grazing on fine roots due to switching to feeding on roots when interspecific competition became more severe at higher Collembola diversity. Furthermore, reduced root biomass may have been due to increased nutrient mobilization in presence of Collembola (Visser et al. 1981, Bardgett et al. 1993c, Scheu et al. 1999, Endlweber and Scheu 2007, Eisenhauer et al. 2010c). Interestingly, Collembola diversity thereby changed root depth distribution in a plant functional group specific way. This adds a novel mechanism how Collembola affect plant competition and performance. In contrast to grasses, net shoot and root productivity of herbs was at maximum in treatments with three Collembola species, most likely due to effects of both compensatory plant growth and increased nutrient availability induced by Collembola grazing. The assumption that elevated N supply contributed to the observed Collembola effect is supported by increased ^{15}N uptake by herbs in Heteromurus only treatments and in the presence of three Collembola species.

3.6 CONCLUSIONS

Results of this study suggest that context dependent interactions among Collembola species influence litter decomposition and plant productivity in non-additive ways. Collembola decelerated soil surface litter decomposition, whereas root litter decomposition

likely was accelerated; both effects were most pronounced in the presence of *Heteromurus*. Collembola diversity changed root depth distribution in a plant functional group specific way indicating distinct changes in plant competition due to changes in Collembola diversity and composition. Idiosyncratic and context dependent effects of Collembola diversity even in rather simple assemblages of one to three species suggest that changes in Collembola diversity may have unpredictable consequences for ecosystem functioning. Our results further suggest that the linkage between Collembola response and effect traits is non-linear confirming recent findings for plants (Suding et al. 2008).

Chapter 4

Soil Organisms shape the Competition between Grassland Plant Species

4.1 ABSTRACT

Arbuscular mycorrhizal fungi (AMF) and decomposers determine plant nutrition, however, little is known about interactive effects of AMF and decomposers on plant communities. We set up a greenhouse experiment to study effects of plant competition (one and two-species treatments), Collembola (*Heteromurus nitidus* and *Protaphorura armata*) and AMF (*Glomus intraradices*) on the performance (above- and belowground productivity and nutrient uptake) of three grassland plant species (*Lolium perenne*, *Trifolium pratense* and *Plantago lanceolata*) representing three dominant plant functional groups (grasses, legumes and herbs). Further, we investigated variations in Collembola performance and AMF colonization rates of plant roots. Generally, *L. perenne* benefited from being released from intraspecific competition in the presence of *T. pratense* and *P. lanceolata*. The presence of AMF increased the competitive strength of *P. lanceolata* and *T. pratense* against *L. perenne* and also modified the effects of Collembola on plant productivity. The colonization of roots by AMF was reduced in treatments with two plant species suggesting that plant infection by AMF was modified by interspecific plant interactions. Collembola did not affect total colonization of roots by AMF but increased the number of mycorrhizal vesicles in *P. lanceolata*. AMF and Collembola both enhanced the amount of N and P in plant shoot tissue, but impacts of Collembola were less pronounced in the presence of AMF. Overall, the results suggest that, by differentially affecting the performance and nutrient acquisition of plant species, AMF and Collembola interactively modify plant competition and shape the composition of grassland plant communities. The results suggest that plant community composition can only be understood when complex belowground interactions are considered.

4.2 INTRODUCTION

Competition between plants is an important factor determining the composition of terrestrial plant communities (Aerts 1999). Although aboveground competition for light and space is most apparent, belowground competition among plant species for soil nutrients and water also plays an important role for plant community assembly (Aerts 1999, Cahill 1999). Recent studies even suggest that belowground competition of plant roots is more important for the structure of plant communities than aboveground interactions (Weigelt et al. 2007,

Eisenhauer et al. 2009a). Generally, plants respond to belowground competition by increased production of roots at the expense of shoot biomass (Maina et al. 2002). However, the response of plants to inter- and intraspecific competition, vary with root architecture and plant species identity (Lodge 2000, Endlweber and Scheu 2007). Particularly grasses have been found to be superior competitors for soil nutrients (Munoz and Weaver 1999, Eisenhauer and Scheu 2008). Plant nutrition depends on a variety of factors with symbiosis of plant roots with mycorrhizal fungi being among the most important (Smith and Read 1997, Van der Heijden et al. 1998).

Arbuscular mycorrhizal fungi (AMF) are the dominant mycorrhizal fungi in grassland ecosystems improving plant nutrition by extending the surface area of plant roots for nutrient capture by forming an extensive network of extraradical hyphae (Smith and Read 1997). This network in particular improves plant uptake of phosphorous but also that of nitrogen (Marschner and Dell 1994, Smith and Read 1997, Hawkins et al. 2000). Typically, these elements limit plant growth in terrestrial ecosystems and therefore their availability determines competition between plant species (Van der Heijden et al. 2003, Scheublin et al. 2007).

AMF, however, are imbedded in a complex food web of microbivore invertebrates, such as springtails (Collembola), and this likely modifies their functioning (Moore et al. 1987). Although soil microbivores stimulate nutrient mineralization and thereby resource availability for plants (Rusek 1998, Scheu et al. 1999, Gange 2000), their role for plant competition and community assembly has been largely neglected (but see e.g. Endlweber and Scheu 2007, Eisenhauer et al. 2010a, 2011b).

Collembola are a major component of the decomposer fauna in many terrestrial ecosystems (Bardgett et al. 1993, Hopkin 1997), reaching densities of up to 60,000 ind./m² in grasslands (Gange and Bower 1997). Although most Collembola are considered to be primarily fungivorous (Hopkin 1997, Coleman et al. 2004), they are trophically diverse with some species feeding on living plant tissue, including plant roots (Hurej et al. 1992, Rusek 1998, Endlweber et al. 2009). By mobilizing nutrients from fungal and bacterial biomass Collembola affect plant nutrition (Ineson et al. 1982, Harris and Boerner 1990, Pieper and Weigmann 2008) and therefore the competitive relationship between plant species (Kreuzer et al. 2004, Endlweber et al. 2006, Endlweber and Scheu 2007). Collembola may play an important role in the interrelationship between AMF and their host plants, and the few previous studies suggest that the interactions between Collembola and AMF are complex

(Klironomos and Kendrick 1996). Feeding of Collembola on AMF may decrease the colonization of roots by AMF, thereby reducing plant nutrient uptake and plant growth (Finlay 1985, Harris and Boerner 1990, Fitter and Sanders 1992). At low densities, however, Collembola may stimulate AMF growth and development presumably by grazing on senescent hyphae and mobilizing the nutrients therein (Harris and Boerner 1990, Gange and Ayres 1999). In addition, Collembola may also increase mycorrhizal root colonization by transporting spores and hyphae adhering to their body surface (Klironomos and Moutoglis 1999). However, effects of Collembola on plant growth have been shown to not only vary with Collembola numbers, but also with species identity of Collembola, AMF and plants (Harris and Boerner 1990, Scheu et al. 1999, Gange 2000). Therefore, Collembola and AMF likely interactively affect competitive relationships between plant species.

To investigate the relationship between Collembola, AMF and plant species we studied the interactive impacts of Collembola and AMF on the performance of grassland plant species belonging to different functional groups (grasses, herbs and legumes). Further, we studied the effect of plant species identity and the presence of Collembola on the colonization of roots by AMF, and effects of the presence of AMF on the density of Collembola. Specifically, we hypothesized that (1) Collembola performance and mycorrhizal colonization of roots vary with plant species, and (2) Collembola and AMF interactively affect plant nutrition and growth. Further, we expected (3) effects of Collembola and AMF to vary depending on plant species resulting in changes in the competitive strength of plant species.

4.3 MATERIALS AND METHODS

EXPERIMENTAL SETUP

The experiment was conducted in a temperature-controlled greenhouse at a day/night regime of 16/8 h and 20/16 ± 2ºC with light intensity varying between 450 and 650 µE $m^{-2} \cdot s^{-1}$ depending on weather conditions (Fig. 4.1A). We set up microcosms consisting of PVC tubes (inner diameter 8 cm, height 20 cm) covered by a 1 mm mesh at the bottom to allow drainage of water. A plastic barrier (10 cm height) was attached on top of each microcosm to prevent Collembola from escaping (Fig. 4.1B). Microcosms were filled to a height of 15 cm with 1.5 kg (fresh weight) of sieved (2 mm) and homogenized soil (equivalent to 1.25 kg dry weight). The soil (pH 8.1, carbon content 4.6%, nitrogen content 0.3%, C-to-N ratio 15.7, gravimetric

water content 17%) was taken from the south-eastern edge of the Jena Experiment field site (Roscher et al. 2004) and autoclaved twice for each 20 min at 120°C. To leach nutrients from the soil made available by the defaunation process, microcosms were irrigated with 50 ml of deionized water per day for 10 days prior to the start of the experiment.

AMF inoculum (10 g culture substrate mixed with hyphae and spores of *Glomus intraradices* Schenck & Smith; Sybio-m s.r.o., Lanskroun, Czech Republic) was added to half of the microcosms by mixing the inoculum with the upper 5 cm of the soil. Fresh soil (500 g) from the field site of the Jena Experiment was suspended in 1.5 l deionized water and sequentially filtered through 100, 50 and 11 µm mesh to exclude spores and larger hyphal fragments of mycorrhizal fungi. Deionized water was added to the suspension to obtain 3 l of inoculation solution; 15 ml of this solution was added to each microcosm to re-establish bacterial communities resembling those in the field.

Three plant species belonging to three plant functional groups (*Lolium perenne* L., *Plantago lanceolata* L. and *Trifolium pratense* L., representing grasses, herbs and legumes, respectively) were selected from the species pool of the Jena Experiment (Roscher et al. 2004) and grown from seeds in pots filled with autoclaved Jena soil in the greenhouse for three weeks to a height of approx. 5 cm. Legume seeds were mechanically scarificated to stimulate germination. The seeds were purchased from Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany).

In a factorial design experimental approach, four plant seedlings were transplanted into each microcosm to establish three plant monocultures (*L. perenne*, *P. lanceolata*, *T. pratense*) and three two-species treatments, comprising every possible two-species combination, each consisting of two plant individuals for each plant species. Notably, using one representative species from three plant functional groups, we cannot differentiate plant identity from functional identity effects. However, the main objective of the present study was to investigate potential changes in competition of functionally distinct plant species in response to the presence of and interactions among AMF and Collembola.

After transplanting the seedlings, the microcosms were watered every second day (50 ml portions of deionized water); germinating weeds were removed over a period of 14 d. Subsequently, 20 medium-sized adult individuals of each *Heteromurus nitidus* (Templeton 1835) and *Protaphorura armata* (Tullberg 1869) from laboratory cultures were added to half of the microcosms to establish two Collembola treatments (with and without). Each treatment

was replicated five times resulting in a total of 120 microcosms, which were placed in the greenhouse and randomized every week to avoid edge effects.

To simulate natural conditions and to follow litter N uptake by the plants, 400 mg of dried ^{15}N labeled *L. perenne* litter material (40 atom% ^{15}N, carbon concentration 35.8%, nitrogen concentration 1.5%, C-to-N ratio 24.7, cut into ca. 1 cm pieces) was placed on top of the soil after the addition of Collembola. Microcosms were irrigated daily with an increasing quantity of deionized water (initially 35 ml every two days, after 10 weeks up to 150 ml per day) according to the requirements of the growing plants. Each pot received the same amount of water in order to avoid confounding effects of differences in water addition.

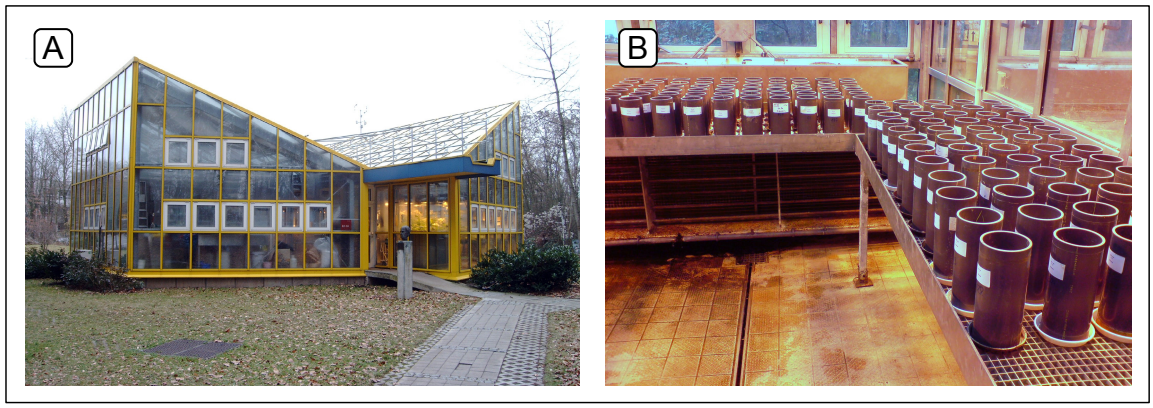

Figure 4.1 Photographs of the experimental setup. (**A**) Photograph of the experimental greenhouse. (**B**) Arrangement of the 120 microcosms in one of the climate chambers of the greenhouse prior to the start of the experiment. (Photographs by A. Sabais).

SAMPLING AND ANALYTICAL PROCEDURES

After 12 weeks, plant shoots were harvested by cutting shoots at soil surface level. Plant shoots were separated to species, dried at 70°C for 3 d and weighed. The soil cores were removed from the microcosms and Collembola were extracted by heat (Kempson et al. 1963). Collembola species were identified and counted. Roots were washed out of the soil using a 1 mm mesh, dried at 70°C for 3 d, and weighed; it was not possible to separate roots of plant species. However, a plant species-specific subsample of roots (2.20 ± 0.11 g dry weight) was fixed in formaldehyde-acetic acid [FAA; 6.0% formaldehyde, 2.3% glacial acetic acid, 45.9% H_2O, 45.8% ethanol (v/v)] to analyze the colonization of roots by AMF. For staining of

mycorrhiza, roots were incubated in 10% KOH at 95°C for 10-15 min (*P. lanceolata* 10 min, *L. perenne* 15 min), rinsed with tap water and acidified with 3.7% HCl for 5 min (Phillips and Hayman 1970). For staining of roots, a staining solution consisting of 5% ink diluted in vinegar (5% acetic acid) was used. For decolorization and short time storage, roots were deposited in tap water (Vierheilig and Piche 1998). Percentage colonization of root length (total, arbuscules and vesicles) was determined using the line intersect method (Ambler and Young 1977; modified after Schmitz et al. 1991) and a Zeiss Axioplan microscope at 100ξ magnification. At least 200 segments of each root sample were counted.

We analyzed nutrients in plant shoot tissue of *P. lanceolata* and *T. pratense* since the performance of these two species was affected most by our treatments. Approximately 3.5 mg of the powdered plant shoot material of *P. lanceolata* and *T. pratense* was weighed into tin capsules. Total N concentrations and ^{15}N signatures were determined by a coupled system consisting of an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) and a gas isotope mass spectrometer (MAT 251, Finngan, Bremen, Germany; Reineking et al. 1993). For ^{15}N atmospheric N_2 served as the primary standard and acetanilide (C_8H_9NO; Merck, Darmstadt, Germany) was used for internal calibration.

Total P concentration of ground plant shoot material of *P. lanceolata* and *T. pratense* was analyzed using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES, PerkinElmer, Rodgau-Jügesheim, Germany). Samples were dissolved in concentrated nitric acid and heated in a microwave system at 230°C for 20 min. Then, total P was measured in a Spectro Ciros ccd (Spectro Analytical Instruments GmbH, Kleve, Germany) at two different wave length (177.4 nm and 178.3 nm) according to the EC Guideline EN ISO 11885. The amount of total shoot N and P per microcosm was calculated by multiplying shoot biomass with the N and P concentrations of the corresponding plant species.

STATISTICAL ANALYSIS

Prior to statistical analysis data on Collembola numbers and plant biomass were log-transformed ($\log_{10}[x + 1]$), if necessary, to meet the requirements of analyses of variance (ANOVA). Means presented in the text and figures were calculated using non-transformed data (± standard error). Comparisons of means were performed using Tukey's honestly significant difference test ($\alpha = 0.05$).

ANOVA as part of the general linear model (GLM, type I sum of squares) was used to analyze the effects of plant species diversity (DIV; monocultures and two-species treatments),

plant species identity (LOL, *L. perenne*; PLA, *P. lanceolata*; TRI, *T. pratense*), Collembola (COL; with and without *H. nitidus* and *P. armata*), and AMF (with and without *G. intraradices*) on shoot biomass, root biomass, total plant biomass per microcosm and shoot-to-root ratio in sequential analyses. DIV was fitted first, followed by the single plant species (LOL, PLA, TRI), COL and AMF. Thereafter, the interactions between COL*AMF and COL*DIV were analyzed. Finally, interactions of COL, AMF and individual plant species were calculated. Variables containing any of the single plant species were fitted separately for every response variable in the order of their explanatory value (determined in additional analyses fitting the respective variable first), and the variable with the lowest explanatory value was excluded from the final model. Using the same model, we analyzed the effects of DIV, LOL, PLA, TRI, AMF and the interaction between DIV*AMF, and the effects of AMF and plant species on the density of *H. nitidus*, *P. armata* and total Collembola per microcosm (only treatments with Collembola). Further, GLM (type III sum of squares) was used to analyze the effects of COL, AMF and plant community (COM; monocultures and all possible two-species combinations of the three plant species) on the shoot biomass per individual of *L. perenne*, *P. lanceolata* and *T. pratense.* The same model was used to analyze effects of COL and COM on the colonization of roots by *G. intraradices*, numbers of arbuscules and vesicles of roots of *L. perenne*, *P. lanceolata* and *T. pratense*, and effects of COL and AMF on root biomass of *L. perenne*, *P. lanceolata* and *T. pratense* in monocultures (only microcosms containing AMF).

Finally, GLM (type I sum of squares) was used to analyze effects of plant species identity (PLA, TRI), COL and AMF, and the interactions of COL, AMF and plant species on shoot N concentration, ^{15}N value of shoots, amount of N per microcosm, shoot P concentration and the amount of P per microcosm (for *P. lanceolata* and *T. pratense* only).

4.4 RESULTS

MYKORRHIZA

Root mycorrhization strongly depended on plant species identity, while the presence of Collembola modified colonization rates in some cases. Colonization of plant roots by *G. intraradices* in microcosms without AMF was negligible (0.43 ± 0.27%) and did not depend on the presence of Collembola. In treatments with AMF mycorrhization of plant roots was

higher in *T. pratense* (87 ± 3%) and *P. lanceolata* (85 ± 4%) than in *L. perenne* (43 ± 4%; Table 4.1). The presence of Collembola did not significantly affect total mycorrhization rates of the plants, but significantly increased the number of mycorrhizal vesicles in *P. lanceolata* by +29% (Table 4.1). The type of plant community significantly affected mycorrhizal parameters in each of the three plant species (Table 4.1). The number of arbuscules in *L. perenne* was significantly reduced (-85%) in the presence of *T. pratense*. Also, in the presence of *P. lanceolata* the number of arbuscules in *L. perenne* was reduced, but only in the treatment with Collembola (-76%). Further, the presence of *T. pratense* significantly reduced the number of arbuscules (-42%), but increased the number of vesicles in *P. lanceolata* (+25%). By contrast, the presence of *L. perenne* reduced vesicle numbers in *P. lanceolata* by -20%. Moreover, the presence of *L. perenne* significantly reduced the mycorrhization rate and the number of arbuscules in *T. pratense* by -19% and -41%, respectively, whereas the presence of *P. lanceolata* significantly reduced the number of arbuscules by -45%.

COLLEMBOLA

Generally, the density of Collembola depended on complex interactions between plant identity and presence of AMF. Numbers of Collembola increased 13-fold during the experiment to a total of 522 ± 42 individuals per microcosm in Collembola treatments, with *P. armata* dominating the community (78% of total). Neither plant species diversity nor AMF significantly affected Collembola density (Table 4.2). However, depending on the presence of AMF, Collembola density was significantly affected by the presence of T. pratense and P. lanceolata, but not by *L. perenne* (Table 4.2, Fig. 4.2). In treatments with *T. pratense* Collembola numbers were increased by +72% in the absence of AMF, whereas they were decreased by -40% in the presence of AMF (Fig. 4.2a). In contrast, in treatments with P. lanceolata the number of *P. armata* was decreased in the absence of AMF (-24%), but increased in the presence of AMF (+79%; Fig. 4.2b). Further, the density of H. nitidus was increased significantly in presence of *T. pratense* (+57%).

Table 4.1 ANOVA table of *F*-values for the effects of Collembola (COL) and plant community (COM) on mycorrhizal colonization by *Glomus intraradices* [%] and number of arbuscules and vesicles formed in plant roots of *Lolium perenne*, *Plantago lanceolata* and *Trifolium pratense*.

	df	Mycorrhization	Arbuscules	Vesicles
Lolium perenne				
COL	1, 12	0.58	0.50	0.03
COM	2, 12	2.74	**13.29****	2.77
COL∗COM	2, 12	0.20	**6.49***	1.41
Plantago lanceolata				
COL	1, 12	3.56	0.32	**9.28***
COM	2, 12	1.24	**13.17****	**8.98****
COL∗COM	2, 12	1.48	2.41	1.40
Trifolium pratense				
COL	1, 12	0.65	1.62	2.61
COM	2, 12	**4.62***	**4.79***	3.59
COL∗COM	2, 12	0.01	0.39	0.36

Significant effects are given in bold. * = $P < 0.05$, ** = $P < 0.01$.
df, degrees of freedom (treatment, error)

Table 4.2 ANOVA table of *F*-values for the effects of plant species diversity (DIV), *Lolium perenne* (LOL), *Plantago lanceolata* (PLA), *Trifolium pratense* (TRI) and arbuscular mycorrhiza (AMF) on the density of *Heteromurus nitidus*, *Protaphorura armata* and total Collembola per microcosm.

	df	*H. nitidus*	*P. armata*	Total Collembola
DIV	1, 52	0.97	1.51	1.59
LOL	1, 52	0.63	0.20	0.66
PLA	1, 52	excluded	0.63	0.05
TRI	1, 52	3.75	excluded	excluded
AMF	1, 52	0.35	1.88	2.05
AMF∗DIV	1, 52	1.05	0.13	0.92
AMF∗LOL	1, 52	excluded	excluded	excluded
AMF∗PLA	1, 52	0.00	**7.84****	2.45
AMF∗TRI	1, 52	0.29	0.84	**8.02****

Significant effects are given in bold. ** = $P < 0.01$, * = $P < 0.05$.
df, degrees of freedom (treatment, error); 'excluded' indicates terms excluded during model simplification

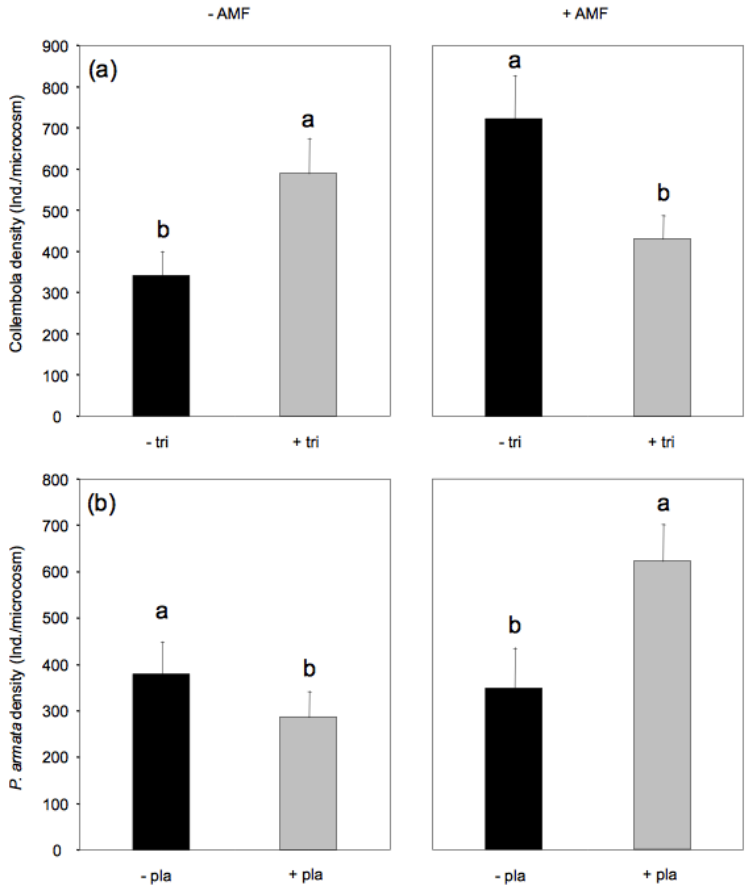

Figure 4.2 Effects of (**a**) *Trifolium pratense* on the density of total Collembola per microcosm and (**b**) *Plantago lanceolata* on the density of *Protaphorura armata* per microcosm as affected by presence of arbuscular mycorrhiza (without [- AMF] and with [+ AMF] *Glomus intraradices*). Means with standard error. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

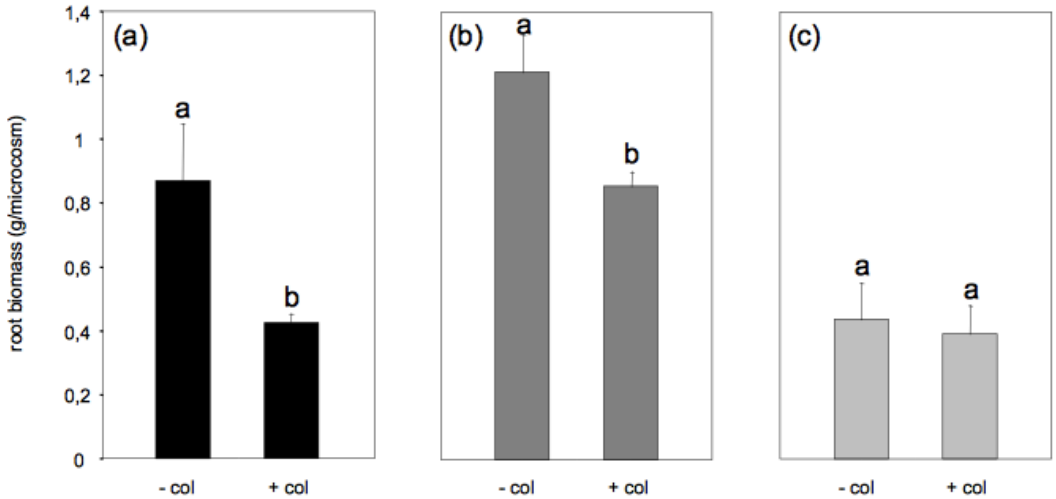

Figure 4.3 Variations in root biomass per microcosm in monocultures of (a) *Lolium perenne*, (b) *Plantago lanceolata* and (c) *Trifolium pratense* as affected by the presence of Collembola (*Heteromurus nitidus* and *Protaphorura armata*; without [- col] and with [+ col]). Means with standard error. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

PLANT PRODUCTIVITY

Plant productivity strongly differed between plant species and depended on competitive interactions among plants; however, AMF and Collembola significantly altered plant competition by favoring certain species and by changing biomass allocation in above- and belowground structures. Presence of *L. perenne* significantly decreased shoot (-42%) and total plant biomass per microcosm (-40%; Table 4.3). By contrast, presence of *P. lanceolata* significantly increased root and total biomass per microcosm by +59 and +41%, respectively. Effects of *T. pratense* on plant productivity depended on the presence of AMF (Table 4.3). In *T. pratense* treatments without AMF, shoot (-23%), root (-44%) and total biomass per microcosm (-35%) were reduced, whereas in treatments with AMF shoot (+76%) root (+19%) and total biomass per microcosm (+46%) were increased. Further, in *T. pratense* treatments plant shoot-to-root ratio was increased by +39%, with the increase being more pronounced when Collembola were present (Table 4.3). AMF significantly increased shoot (+51%), root (+23%) and total biomass per microcosm (+36%), but their presence did not affect plant shoot-to-root ratio. By contrast, presence of Collembola generally increased plant shoot-to-root ratio by +28%, but did not affect total plant biomass. However, effects of Collembola on plant shoot-to-root ratio varied with plant species diversity (Table 4.3). In plant monocultures the presence of Collembola significantly increased plant shoot-to-root ratio by +73%, whereas in two-species treatments it was slightly decreased (-7%). These changes in shoot-to-root ratio corresponded to the reduction in root biomass in plant monocultures (-34%), whereas Collembola did not affect root biomass in two-species treatments. In monocultures the reduction in root biomass only occurred in *L. perenne* (-51%) and *P. lanceolata* (-30%), but not in *T. pratense* (Table 4.4, Fig. 4.3).

Shoot biomass of plant species varied considerably with plant community composition (Table 4.5, Fig. 4.4). As compared to monocultures, shoot biomass of *L. perenne* was significantly increased in the presence of both *P. lanceolata* (+68%) and *T. pratense* (+69%; Fig. 4.4a). Further, the presence of *T. pratense* increased shoot biomass of *P. lanceolata* (+62%), whereas the presence of *L. perenne* decreased it (-86%; Fig. 4.4b). However, both effects were less pronounced in treatments with than in those without AMF. Shoot biomass of *T. pratense* was significantly reduced in microcosms with *P. lanceolata* (-32%) and *L. perenne* (-73%; Fig. 4.4c). However, the effects depended on the presence of AMF; in treatments without AMF shoot biomass of *T. pratense* was significantly decreased by both *L. perenne* and *P. lanceolata*, whereas in the presence of AMF only *L. perenne* significantly

decreased shoot biomass of *P. lanceolata*. The presence of Collembola did not affect shoot biomass of *L. perenne* and *T. pratense*, but significantly increased that of *P. lanceolata* (+14%). Further, AMF significantly increased shoot (+1052%) and root biomass (+436%) of *T. pratense*.

Table 4.3 ANOVA table of *F*-values for the effects of plant species diversity (DIV), *Lolium perenne* (LOL), *Plantago lanceolata* (PLA), *Trifolium pratense* (TRI), Collembola (COL) and arbuscular mycorrhiza (AMF) on plant shoot biomass, root biomass, total biomass and shoot-to-root ratio.

	df	Shoot biomass	Root biomass	Total biomass	Shoot-to-root ratio
DIV	1, 104	0.23	1.66	1.01	0.46
LOL	1, 104	**75.76*** **	3.54	**11.52*** **	excluded
PLA	1, 104	3.24	**43.01*** **	**39.52*** **	2.27
TRI	1, 104	excluded	excluded	excluded	**20.75****
COL	1, 104	3.77	3.09	0.08	**14.68****
AMF	1, 104	**57.10*** **	**13.92****	**29.48*** **	0.10
COL∗AMF	1, 104	0.87	0.43	0.00	1.87
COL∗DIV	1, 104	0.85	**4.88***	1.00	**17.12*** **
COL∗LOL	1, 104	0.03	0.25	0.38	excluded
COL∗PLA	1, 104	excluded	excluded	excluded	0.20
COL∗TRI	1, 104	0.12	0.01	0.12	**5.07***
AMF∗DIV	1, 104	2.96	0.00	0.76	0.43
AMF∗LOL	1, 104	0.16	0.13	0.13	excluded
AMF∗PLA	1, 104	excluded	excluded	excluded	0.19
AMF∗TRI	1, 104	**79.99*** **	**22.41*** **	**45.94*** **	0.11
DIV∗COL∗AMF	1, 104	0.62	0.41	0.01	2.55
COL∗AMF∗LOL	1, 104	2.52	1.86	2.55	0.01
COL∗AMF∗PLA	1, 104	excluded	excluded	excluded	0.00
COL∗AMF∗TRI	1, 104	0.17	0.62	0.49	excluded

Significant effects are given in bold; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$
df, degrees of freedom (treatment, error); 'excluded' indicates terms excluded during model simplification

Table 4.4 ANOVA table of *F*-values for the effects of Collembola (COL), arbuscular mycorrhiza (AMF) and plant community (COM) on root biomass of *Lolium perenne*, *Plantago lanceolata* and *Trifolium pratense* in monocultures.

	df	Root biomass		
		Lolium perenne	*Plantago lanceolata*	*Trifolium pratense*
COL	1, 50	**11.67****	**8.20***	0.49
AMF	1, 50	3.59	0.21	**161.01*****
COL∗AMF	1, 50	**7.04***	0.17	3.46

Significant effects are given in bold; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$
df, degrees of freedom (treatment, error)

Table 4.5 ANOVA table of *F*-values for the effects of Collembola (COL), arbuscular mycorrhiza (AMF) and plant community (COM) on shoot biomass of *Lolium perenne*, *Plantago lanceolata* and *Trifolium pratense*.

	df	Shoot biomass		
		Lolium perenne	*Plantago lanceolata*	*Trifolium pratense*
COL	1, 50	1.31	**8.86****	0.03
AMF	1, 50	0.28	0.87	**407.15*****
COM	2, 50	**25.95*****	**599.61*****	**52.85*****
COL∗AMF	1, 50	0.48	0.03	3.17
COL∗COM	2, 50	0.11	0.75	3.31
AMF∗COM	2, 50	0.43	**10.50****	**17.16*****

Significant effects are given in bold; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$
df, degrees of freedom (treatment, error)

Table 4.6 ANOVA table of *F*-values for the effects of plant species (PLANT; *Plantago lanceolata* and *Trifolium pratense*), Collembola (COL) and arbuscular mycorrhiza (AMF) on concentrations and amounts of plant nutrients in *P. lanceolata* and *T. pratense* (shoot N concentration [%], amount of shoot N per microcosm [mg], atom%^{15}N, shoot P concentration [%], amount of shoot P per microcosm [mg]).

Variable	N concentration	N amount	atom% ^{15}N	P concentration	P amount
PLANT	**513.31*** **	**15.55*** **	**87.15*** **	**9.91** **	**11.26** **
COL	1.17	**9.07** **	0.02	1.21	**11.46** **
AMF	1.15	**59.29*** **	**50.73*** **	**7.55** **	**54.34*** **
PLANT∗COL	1.60	2.98	0.42	1.14	3.15
PLANT∗AMF	2.87	**95.16*** **	**59.17*** **	**10.36** **	**69.24*** **
COL∗AMF	0.02	**5.32***	0.70	0.55	**7.03***
PLANT∗COL∗AMF	0.75	2.84	3.90	0.12	3.65

Significant effects are given in bold; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$
Degrees of freedom for each treatment and treatment interaction = 1, for error = 32

NUTRIENTS IN PLAT SHOOT TISSUE

Nutrient concentrations and amounts in shoot tissue as well as N uptake differed significantly between plant species and depended on the presence of AMF, Collembola and partly on interactions among them. Shoot tissue concentrations of nitrogen (N; 0.72 ± 0.02%, -164%) and phosphorus (P; 0.084 ± 0.03%, -19%), and the amount of shoot N (5.87 ± 1.05 mg, -61%) were significantly lower in *P. lanceolata* than in *T. pratense.* By contrast, ^{15}N values in shoots of *P. lanceolata* (1.02 ± 0.04 atom%) significantly exceeded that in *T. pratense* by +82% (Table 4.6).

The effect of AMF on ^{15}N values and P concentrations in plant shoots varied with plant species identity. In *P. lanceolata* shoot ^{15}N value and P concentration were not affected by AMF, whereas in *T. pratense* the presence of AMF significantly reduced shoot ^{15}N value and P concentration by -83% and -26%, respectively (Table 4.6). Generally, AMF did not significantly affect shoot N concentrations. However, AMF significantly increased the amount

of shoot N (+469%) and P (+341%) per microcosm in treatments with *T. pratense*, but AMF did not significantly affect the amount of shoot N and P in treatments with *P. lanceolata*. Notably, in treatments without AMF the amount of shoot N and P in *P. lanceolata* exceeded that in *T. pratense*.

Collembola did not significantly affect shoot N and P concentrations as well as shoot ^{15}N values, but significantly increased the amount of shoot N and P per microcosm. This effect, however, varied with the presence of AMF (Table 4.6, Fig. 4.5). In treatments without AMF Collembola significantly increased shoot N and P by +74% and +55%, respectively, whereas in treatments with AMF Collembola only little affected the amount of shoot N and P per microcosm.

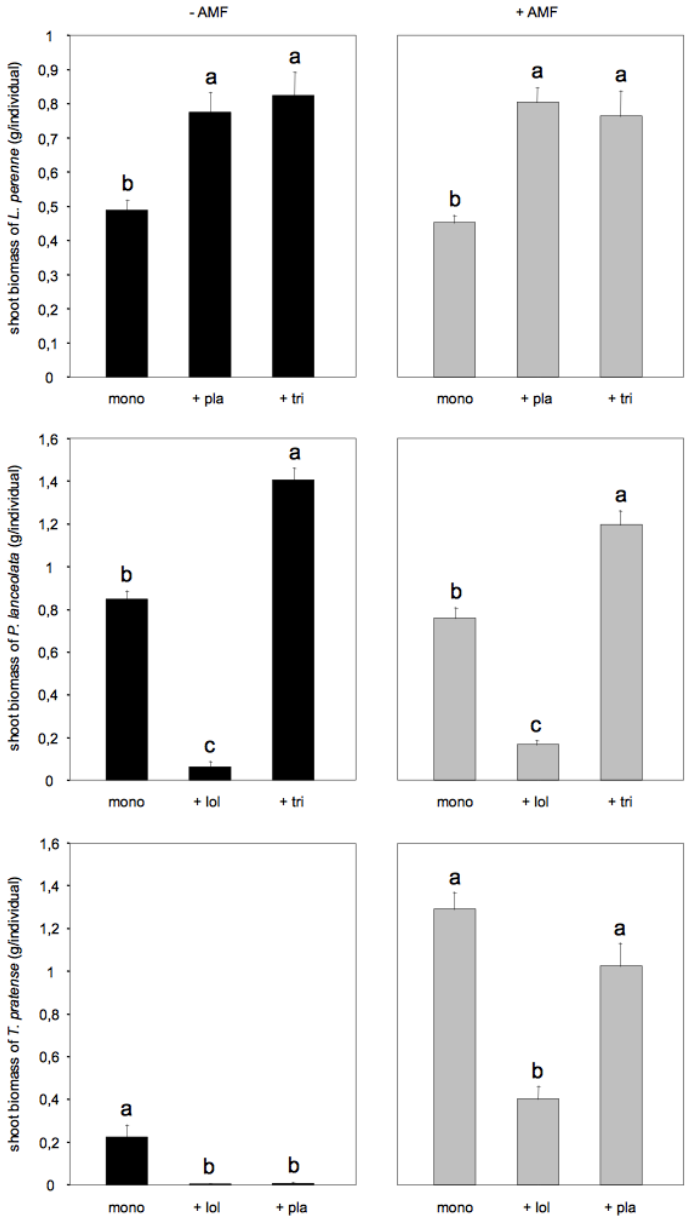

Figure 4.4 Effects of plant community (monocultures [mono], two-species treatment with *Lolium perenne* [+ lol], two-species treatment with *Plantago lanceolata* [+ pla], two-species treatment with *Trifolium pratense* [+ tri]) on shoot biomass per individual of (a) *Lolium perenne,* (b) *Plantago lanceolata* and (c) *Trifolium pratense* as affected by presence of arbuscular mycorrhiza (*Glomus intraradices*; without [- AMF] and with [+ AMF]). Means with standard error. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

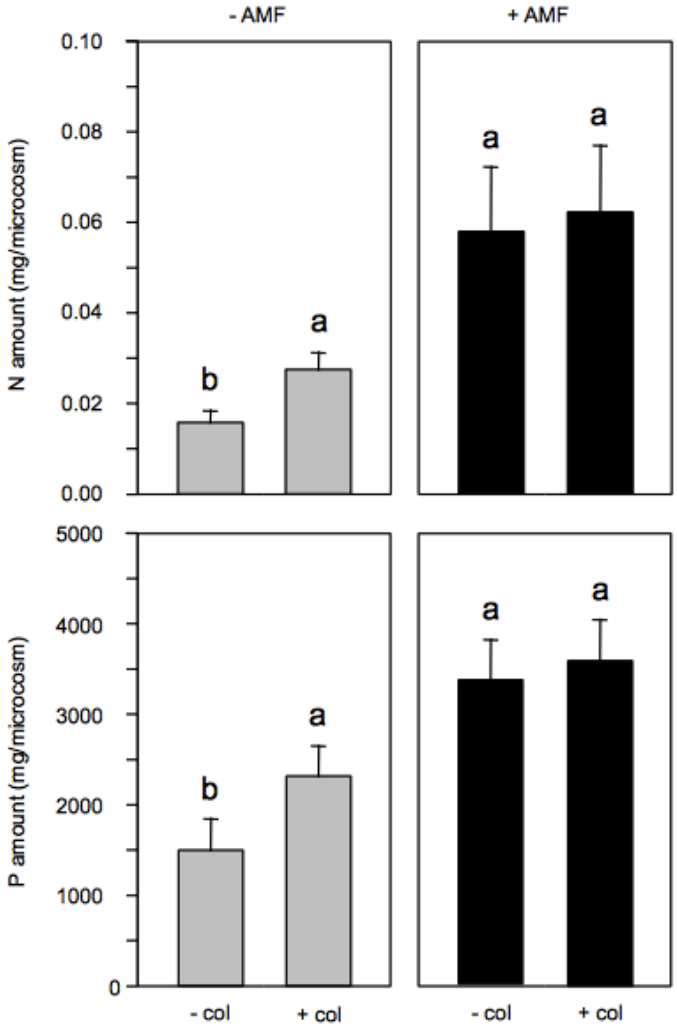

Figure 4.5 Effects of Collembola (*Heteromurus nitidus* and *Protaphorura armata*; without [- col] and with [+ col]) on the amount of shoot N and shoot P per microcosm as affected by the presence of arbuscular mycorrhiza (*Glomus intraradices*; without [- AMF] and with [+ AMF]). Means with standard error. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

4.5 DISCUSSION

MYKORRHIZA

In agreement with our hypothesis (1), mycorrhization of plant roots differed considerably between plant species, with *L. perenne* being less colonized than *P. lanceolata* and *T. pratense*. This coincides with previous observations by Scheublin et al. (2007) and Eisenhauer et al. (2009b) who found root colonization by AMF to be higher in legumes than in grasses. However, colonization of roots by mycorrhiza of plant monocultures differed markedly from that in two-species mixtures of plants, with mycorrhizal infection being generally reduced in plants exposed to interspecific competition. Reduced shoot ^{15}N and P concentrations in *P. lanceolata* and *T. pratense* in two-species treatments as compared to

monocultures suggest that AMF and plant roots competed for nutrients in soil or that plant species competing for resources allocated less carbon to mycorrhizal fungi. Recent studies indeed reported competitive and antagonistic interactions between mycorrhizal and saprotrophic fungi (Baar and Stanton 2000, Tiunov and Scheu 2005b) with the balance depending on the environmental context (Hoeksema et al. 2010). Wurst et al. (2004) suggested competition for soil nitrogen between *G. intraradices* and roots of *P. lanceolata*.

COLLEMBOLA

In agreement with our hypothesis (1), Collembola density varied with plant species identity but the effect depended on the presence of mycorrhiza. Collembola numbers were increased in presence of *T. pratense* without AMF, whereas they were decreased in the presence of AMF. By contrast, the opposite was true for the numbers of *P. armata* in treatments with *P. lanceolata* without and with AMF. The differential response of Collembola to the presence of AMF in the varying plant species treatments may be due to a mycorrhiza-induced alteration of carbon compounds sequestered into the rhizosphere as observed by Kempel et al. (2010). The decomposer system strongly relies on plant-derived carbon sources entering the belowground system via dead plant materials and root exudates, and results of recent studies suggest that root-derived resources form an essential component of the diet of decomposer biota, such as soil microorganisms, Collembola and earthworms (Milcu et al. 2006, Endlweber et al. 2009, Eisenhauer et al. 2009b, 2010a).

PLANT PERFORMANCE

Belowground competition between plants for nutrients is a major factor structuring plant communities (Aerts 1999, Weigelt et al. 2007, Eisenhauer et al. 2009a). Correspondingly, *L. perenne* significantly reduced shoot biomass of *P. lanceolata* and *T. pratense* in two-species mixtures. Furthermore, the biomass of individual shoots of *L. perenne* was increased in two-species treatments as compared to monocultures. This competitive superiority of *L. perenne* is in line with previous studies (Munoz and Weaver 1999, Endlweber and Scheu 2007, Eisenhauer and Scheu 2008) and is likely due to the extensive fine root system of grasses allowing efficient nutrient exploitation (Stone et al. 1998). Unlike *T. pratense*, *P. lanceolata* depended on soil N as denoted by the high ^{15}N values and thus suffered most from competition with *L. perenne*. However, in the absence of AMF, the competitiveness of *T. pratense* was also low, suggesting that the competitive advantage of

N-fixing legumes is abrogated in soils with high nitrogen availability. Autoclaving soil to eliminate mycorrhiza mobilizes nutrients, in particular nitrogen. Despite leaching of nutrients prior to the start of our experiment, increased levels of N may have contributed to the low competitiveness of *T. pratense*. However, increased shoot growth of *L. perenne* in the presence of *P. lanceolata* and *T. pratense* as compared to conspecifics also suggests that *L. perenne* suffers strongly from intraspecific competition. The higher growth rate of the grass in combination with its highly ramified root system may have intensified competition in the limited space of the microcosms when grown in monoculture.

Mycorrhizal fungi may alter competitive relationships between plant species by changing plant nutrient availability and uptake (Van der Heijden et al. 2003, Scheublin et al. 2007, Wagg et al. 2011) which is supported by the results of the present study. Conform to our hypothesis (3), the impact of AMF on plant competition varied with the identity of the competing plant species. Presence of AMF reduced the competitive superiority of *L. perenne* over *P. lanceolata* and *T. pratense*, indicating that AMF predominantly improved nutrient capture of herbs thereby improving their competitive strength against the grass. Supporting this conclusion Scheublin et al. (2007) reported that with increasing nutrient limitation the competitive relationship between plant species shifts towards species with the highest AMF dependency. Compared to grasses, herbs form a less branched and less exploitative root system and therefore are likely to benefit more from AMF presence than grasses. In fact, roots of *T. pratense* and *P. lanceolata* were more intensively colonized by AMF than those of *L. perenne* in the present study. By extending the surface area of plant roots, AMF increase the capture of nutrients by plants, primarily that of N and P (Marschner and Dell 1994, Smith and Read 1997, Hawkins et al. 2000). Correspondingly, the total amount of N and P in treatments with *T. pratense* was increased in presence of AMF. However, presence of AMF also decreased P and ^{15}N concentrations in plant shoots, particularly in *T. pratense*. The reduction in atom% ^{15}N in shoots of *T. pratense* is in line with earlier results (Eisenhauer et al. 2009b) and indicates that *G. intraradices* competes with plant roots for available N (Wurst et al. 2004). The significant reduction of shoot P concentration in *T. pratense*, however, contradicts the view that mycorrhizal fungi predominantly increase plant P supply.

As a fundamental component of the soil mesofauna, Collembola have been shown to affect plant productivity (Kreuzer et al. 2004, Endlweber et al. 2006, Endlweber and Scheu 2007). The most striking effect of Collembola on plant performance in our study was the significant increase in shoot biomass of *P. lanceolata* as well as the reduction in root biomass

in monocultures of *L. perenne* and *P. lanceolata* and the accompanying increase in plant shoot-to-root ratio. By contrast, root biomass of *T. pratense* remained unaffected, which is in line with results of Eisenhauer et al. (2011b) who found legume communities to be unresponsive to Collembola presence. Furthermore, Scheu et al. (1999) reported Collembola to disproportionately reduce root mass of the grass *Poa annua* in comparison to that of the legume *T. pratense*. Remarkably, even though Collembola reduced root biomass of both *L. perenne* and *P. lanceolata*, the reduction was more pronounced in *L. perenne.* Therefore, Collembola not only increased shoot growth of *P. lanceolata*, but also detrimentally affected the competitive strength of *L. perenne*, presumably by selective feeding on grass roots (Hurej et al. 1992, Rusek 1998, Endlweber et al. 2009). This dietary switch may have been promoted by an increased production of secondary plant metabolites by *P. lanceolata* and *T. pratense*. In addition, AMF have been shown enhance plant resistance against belowground herbivores by enabling their host to allocate more resources into defense compounds (Kempel et al. 2010). Since roots of *P. lanceolata* and *T. pratense* were more densely colonized by AMF than those of *L. perenne*, an increased production of defense compounds may have repelled Collembola, forcing them to switch their diet towards the comparatively nutrient-poor roots of the grass. This conclusion is supported by previous studies reporting Collembola to reduce the competitive superiority of *L. perenne* over other plant species (Kreuzer et al. 2004, Partsch et al. 2006, Endlweber and Scheu 2007).

In addition to direct effects on plant performance, Collembola may affect plant growth indirectly via the mobilization of nutrients bound in soil and fungal hyphae or by changing the composition of the microbial community in the rhizosphere (Ineson et al. 1982, Harris and Boerner 1990, Pieper and Weigmann 2008). Consistent with these findings, Collembola increased the total amount of shoot N and P, but did not affect shoot nutrient concentrations. Increased plant growth presumably resulted from enhanced nutrient mineralization in presence of Collembola. Additionally, Collembola grazing on soil fungi might have changed the composition of the fungal community favoring species beneficial to *P. lanceolata* and *T. pratense* as observed for other plant species (Curl et al. 1988, Hiol et al. 1994).

While Collembola enhance nutrient mineralization and availability in soil, AMF increase the potential of their plant host to mobilize these nutrients. Hence, Collembola and AMF affect plant nutrient acquisition by different but concordant mechanisms. In agreement with our hypothesis (2), Collembola and AMF interacted in affecting the total amount of shoot N and P. In treatments without AMF, Collembola significantly increased the total amount of

shoot N and P, whereas in treatments with AMF, they affected shoot nutrient concentrations only little. Presumably, Collembola increased plant nutrient supply by mobilizing soil N and P, but the effect was superseded by the increased plant nutrient capture in the presence of AMF. Potentially, instead of transferring Collembola-mobilized nutrients to the plant, AMF might have used them for hyphal growth.

4.6 CONCLUSIONS

The results of the present study demonstrate that AMF and decomposer soil animals (Collembola) interact in affecting plant competition. Presence of AMF modulated plant specific effects on Collembola and increased the competitiveness of *P. lanceolata* and *T. pratense* against *L. perenne*. While effects of Collembola on plant nutrient acquisition and productivity were superimposed by those of AMF, Collembola increased the amount of nutrients in plant shoot tissue in absence of AMF. Even more, Collembola also enhanced the competitive strength of *P. lanceolata* against *L. perenne*, pointing to a loose inter-kingdom mutualistic relationship between plant, fungus and decomposer soil animals. Therefore, our results show that Collembola and AMF interactively impact the competition between plant species by differentially but concordantly affecting nutrient acquisition of the plant. Thus, if we are to understand the structure of plant communities it is crucial to consider the complex interplay between AMF and decomposer soil animals in shaping plant competition.

Chapter 5

General Discussion

5.1 SETTING AND OBJECTIVES OF THIS THESIS

Most indicators of the state of biodiversity show negative trends with no significant reduction in the rate of decline (Global Biodiversity Outlook 3, 2010). And although the **impacts of declining biodiversity on ecosystem functioning** have been a major focus in scientific research during the last decade, there still is an ongoing debate whether their results can contribute to the general understanding of **species richness effects on ecosystem processes** (Mooney 2002). Although there is agreement that biodiversity affects ecosystems in general terms, it remains unclear to which extent it is simply the number of species, the number of functional groups, the particular mixture of species (i.e., the community composition), or just the presence of certain species within a mixture that are responsible for these effects (Schmid et al. 2002, Cardinale et al. 2006). Understanding the **ecological consequences of biodiversity**, however, is a fundamental challenge and necessitates research under controlled environmental conditions in greenhouse experiments as well as in large-scale field experiments suitable to also uncover long-term effects of declining diversity on ecological processes.

The design of the **Jena Experiment** for the first time allowed separating effects of plant species and plant functional group richness from effects of plant functional group identity. Moreover, field sampling of Collembola four years after the establishment of the experimental plots allowed investigating **long-term effects of plant diversity** on the decomposer subsystem (Tilman et al. 2001, Hedlund et al. 2003, Habekost et al. 2008, Eisenhauer et al. 2010a).

Using the experimental design of the Jena Experiment, the present thesis aimed to explore the main **effects of Collembola on plant communities** of varying plant species and plant functional group richness and how plant communities of varying diversity in turn influence the belowground decomposer community. In order to achieve the objectives of this comprehensive approach I present the outcomes of a field study (**Chapter 2**) and two greenhouse experiments (**Chapter 3** and **Chapter 4**) in the following sections before closing this thesis with a holistic synthesis stressing the **conclusions and perspectives** for future investigations of biodiversity and its implications for ecosystem functioning.

5.2 PLANT COMMUNITY EFFECTS ON COLLEMBOLA

Human activities such as land transformation and homogenization of habitats have led to an unprecedented decline in global biodiversity, resulting in significant changes in the diversity and composition of terrestrial plant communities (**Chapter 1**). Plants, however, function as **interconnecting links** between the **aboveground** and the **belowground** system (Scheu 2001, Wardle et al. 2004), mediating direct and indirect interactions between both subsystems such as antagonistic or mutualistic relationships between plants and root biota (**Chapter 4**). Since the soil decomposer community is generally considered to rely on the diversity, quality and availability of plant derived carbon sources entering the belowground system (Chen and Wise 1997, Wardle 2002, Wardle et al. 2004, Milcu et al. 2006b), **Collembola** are likely to be affected by declining plant diversity and the resulting deterioration of resource diversity, quality and quantity (Hooper et al. 2000, Salamon et al. 2004, Eisenhauer et al. 2010).

In fact, results of the present thesis indicate that Collembola are mainly affected by the **identity of plant functional groups** rather than plant species richness or plant functional group richness, highlighting the importance of plant functional groups for the belowground decomposer system (**Chapter 2, Chapter 3**). However, in contrast to previous studies stressing legumes as driving agents of the decomposer system (Mulder et al. 2002, Temperton et al. 2006, Habekost et al. 2008, Milcu et al. 2008, Roscher et al. 2008), results presented in **Chapter 2** highlight the importance of **grasses** as key plant functional group for Collembola, with legumes rather detrimentally affecting Collembola density. By promoting a high microbial biomass (Carpenter-Boggs 2003, Eisenhauer et al. 2010), the pronounced fine root system of grasses likely provides ample food resources for Collembola feeding either directly on grass roots (Hurej et al. 1992, Rusek 1998, Endlweber et al. 2009) or on root associated bacteria and fungi (Bardgett et al. 1993b, Rusek 1998). Additionally, as compared to the less pronounced root system of herbs, the ramified and dense root system of grasses appears to be better suited as habitat space during cold winter and hot summer months in the field. Notably though, the results of **Chapter 3** challenge the conclusion that Collembola benefit from high root biomass of grasses as Collembola density was not correlated with root biomass in the first greenhouse experiment. Rather, Collembola suffered from reduced food resources and decreased soil water content in legume systems, which was attributed to the high biomass production of legumes, exceeding that of grasses by more than a factor of six. Additionally,

Collembola density remained unaffected by presence of *Lolium perenne* in the second greenhouse experiment (**Chapter 4**), while effects of *Trifolium pratense* and *Plantago lanceolata* depended on presence of **arbuscular mycorrhizal fungi (AMF)**. Kempel et al. (2010) demonstrated that infection of plant roots with AMF may alter the type and amount of carbon compounds sequestered into the rhizosphere, thereby affecting root-associated soil biota such as Collembola.

At first glance, therefore, one might think that our experiments show little evidence of species richness effects of grassland plant communities on Collembola and the ecosystem processes driven by them. Considering the significant impact of plant functional groups on Collembola density as well as the differential response of Collembola to the presence of AMF, the present thesis rather seems to support the assumption that positive effects of plant diversity on Collembola performance are due to **sampling effects** than due to **complementarity effects**. Instead, effects mediated by plant species or plant functional group richness seem to interfere with **biotic or abiotic factors** such as habitat modification by earthworm activity (Maraun et al. 1999, Scheu et al. 2002, Wardle 2002, Eisenhauer et al. 2007) or carbon and nutrient pools in soil (Wardle et al 1999), overriding or buffering the more subtle effects mediated by the plant community.

Nevertheless, besides significant temporal changes of plant community effects on Collembola, soil sampling at the field site of The Jena Experiment indeed showed a positive correlation between plant species richness and Collembola diversity (**Chapter 2)**. Moreover, results of **Chapter 2** indicate a distinct **time-lag** of the response of Collembola to manipulations in plant diversity, as has previously been reported for other groups of soil fauna (Wardle 2002, Gastine et al. 2003, Eisenhauer et al. 2010a). Interestingly, the time-lag of impacts of plant **functional identity** on Collembola appears to be shorter than that of **plant species diversity** (Eisenhauer et al. 2010a, 2011a) which may explain the dominance of plant functional group identity effects in the present study. Furthermore, it indicates that effects of plant functional group identity on the belowground system are more immediate whereas effects of species and plant functional group richness take longer to materialize. It has been argued earlier that plant diversity effects on belowground properties may increase with time (Tilman et al. 2001, Habekost et al. 2008) and current studies performed at the field site of The Jena Experiment corroborate this assumption (Eisenhauer et al. 2011a). The authors argued that the relative importance of certain plant functional groups as drivers of the soil decomposer community decrease with time. Therefore, and in contrast to our initial statement,

the present thesis demonstrates that **positive effects of plant diversity on Collembola** performance are indeed due to species complementarity and that, from a long-term perspective, **plant diversity effects on soil biota are more important** than the presence of key plant functional groups.

5.3 COLLEMBOLA EFFECTS ON PLANT COMMUNITIES

Plants and belowground soil biota are embedded in a **complex network** governing essential ecosystem processes by both **direct and indirect interactions** (**Chapter 1**). Direct interactions include, but are not limited to, root feeding and mutualistic interrelationships between plants and root biota such as mycorrhiza. Indirect interactions, usually considered to be most important (Setälä 1995, Klironomos and Kendrick 1995, Lussenhop 1996), affect plant performance by e.g., physical modification of soil properties, propagation of fungal spores or plant seeds by soil animals such as Collembola and the mineralization of nutrients bound in plant residues or fungal biomass. However, most experiments to date have largely focused on plant species diversity alone and excluded variations in the kinds and numbers of belowground soil biota, such as bacteria, fungi and Collembola (Bardgett and Wardle 2010). Yet, these creatures not only comprise the most numerous portion of earth's biota (estimated to at least a quarter of all currently described species; Bardgett and Wardle 2010) but also drive essential ecosystem functions, such as **nutrient cycling** and **turnover of organic matter** (Scheu and Setälä 2002, Coleman et al. 2004, Wardle et al. 2004), thereby affecting plant growth and plant community composition. Despite evidence that decomposer diversity is crucial for decomposition processes and plant nutrient availability (Bardgett and Cook 1998, Bardgett and Shine 1999, Mikola et al. 2002, Heemsbergen et al. 2004, Tiunov and Scheu 2005a), surprisingly little is known about diversity effects of decomposer animals of similar size and life history strategies on plant performance and litter decomposition. However, results of previous studies suggest that interspecific interactions between Collembola species, such as competition and facilitation, may affect ecosystem functioning (Klironomos and Kendrick 1996, Heemsbergen et al. 2004).

The results of the greenhouse experiment presented in **Chapter 3** demonstrate that **Collembola species composition is more important for ecosystem functioning than Collembola diversity** as plant productivity and litter decomposition was not only driven by

certain Collembola species but by pronounced species interactions such as competition for nutrients and facilitation. **Facilitative interactions** between different species have been shown to increase resource consumption (Cardinale et al. 2002), which in turn may lead to increased nutrient mineralization and plant growth. Correspondingly, the results of **Chapter 3** indicate that *Heteromurus nitidus* indeed facilitated resource acquisition for the smaller Collembola species *Folsomia candida* and *Protaphorura armata* by comminution of large litter fragments, thereby beneficially affecting litter decomposition and nutrient availability. The results therefore support the findings of Heemsbergen et al. (2004) and Eisenhauer et al. (2010a) who concluded that species mixtures containing functionally more dissimilar species may result in facilitative interactions and better performance than mixtures with functionally more similar species. This assumption is strengthened by the fact that Collembola species mixtures comprising the functionally similar species *F. candida* and *P. armata* resulted in lower plant productivity, supposedly due to increased **interspecific competition** for food resources and limited decomposition of large litter fragments. In fact, the evaluation of the density and composition of the Collembola communities used in **Chapter 3** points to distinct **niche overlaps** even between species belonging to varying life history groups (Gisin 1943), supported by the observation that a significantly higher proportion of Collembola was found in deeper soil layers in two species mixtures than in monocultures. The results therefore indicate strong competition for food and living space and demonstrate that Collembola are able to avoid competitive exclusion by migrating into deeper soil layers or by switching their diet to **alternative food resources** (Klironomos and Kendrick 1996, Cortet et al. 2003, Jørgensen et al. 2003). As shown in **Chapter 1** and **Chapter 4** of this thesis, Collembola not only feed on dead organic matter and soil microorganisms but also consume living plant tissue and directly graze on plant fine roots (Hurej et al. 1992, Endlweber et al. 2009). Increased Collembola density in deeper soil layers associated with diet switching might have led to increased feeding on fine roots, thereby reducing uptake of nutrients by the plants. Moreover, Collembola changed root depth distribution in a **plant functional group specific** way, indicating distinct **changes in plant competition** due to changes in Collembola diversity and composition.

Indeed, both greenhouse experiments demonstrated that **impacts of Collembola on plant productivity and community composition strongly depend on plant functional group identity (Chapter 3, Chapter 4**). Remarkably though, the combined results suggest that herb communities benefit most from Collembola presence while growth and competitive

performance of grasses turned out to be detrimentally affected. These findings are in line with observations of Eisenhauer et al. (2010b, 2011b) who reported Collembola to mostly affect herbs, but not legumes. **Legumes**, on the other hand, appeared to be rather unresponsive to Collembola presence, which is conform to the findings of Kreuzer et al. (2004) and Endlweber and Scheu (2007) and confirms that legumes, due to their ability to fix atmospheric nitrogen, are little responsive to changes in soil nutrients and thus to decomposer invertebrates. The results of the present thesis therefore emphasize the necessity that the **complex interactions between Collembola and their environment,** including arbuscular mycorrhizal fungi, have to be considered if predictions on ecosystem functioning are to be made.

Arbuscular mycorrhizal fungi (AMF) are the dominant mycorrhizal fungi in grassland ecosystems, improving plant nutrition by extending the surface area of plant roots for nutrient capture, particularly phosphorous (Smith and Read 1997). However, AMF are imbedded in a complex food web of microbivore invertebrates, and grazing on mycorrhizal fungi by Collembola likely affects the mycorrhiza-plant symbiosis and thereby plant growth (Bakonyi et al. 2002). As Collembola mediated changes in nutrient supply have been shown to affect plant growth (**Chapter 3**), Collembola effects on mycorrhizal inoculation and plant competitiveness were investigated in a second greenhouse experiment.

The results presented in the second greenhouse experiment (**Chapter 4**) outline the importance of soil decomposers and arbuscular mycorrhizal fungi (AMF) as drivers of plant competition, again linking plant performance to interactions with and within the decomposer community (**Chapter 3**). **Collembola enhance nutrient mineralization and availability in soil while AMF increase the potential of their plant host to mobilize these nutrients.** Even though effects of Collembola on plant nutrient acquisition and productivity were superimposed by those of AMF, Collembola increased the amount of nutrients in plant shoot tissue in absence of AMF and reduced the competitive superiority of *L. perenne* against *P. lanceolata* by **selective feeding** on grass roots (Hurej et al. 1992, Rusek 1998, Endlweber et al. 2009). **Grazing on mycorrhizal fungi by Collembola** affect the mycorrhiza-plant symbiosis and thereby plant growth (Bakonyi et al. 2002). By investigating Collembola effects on mycorrhizal inoculation and plant competitiveness it was shown that Collembola indeed alter plant competition by reducing the competitive superiority of *L. perenne* against *P. lanceolata* and *T. pratense*, which is in line with the findings of previous studies reporting Collembola to reduce the competitive superiority of *L. perenne* over other plant species

(Kreuzer et al. 2004, Partsch et al. 2006, Endlweber and Scheu 2007). The insights gained in **Chapter 4** therefore point to a loose inter-kingdom **mutualistic relationship between plant, fungus and Collembola**, capable of **altering competitive relationships** within plant communities and even weakening the frequently-observed competitive superiority of grasses (Munoz and Weaver 1999, Endlweber and Scheu 2007, Eisenhauer and Scheu 2008). The results point to the importance of the interrelationship between Collembola and AMF for competition between grassland plant species.

5.4 SYNTHESIS, PERSPECTIVES AND CONCLUSIONS

Within the last decade, research in the field of biodiversity and ecosystem functioning has made has made an enormous progress (Cardinale et al. 2011). Nevertheless, our knowledge on the role of biodiversity for ecosystem functioning is still limited and a multitude of questions and hypotheses remain unsolved. The present thesis provides new insights on the role of Collembola as important drivers of ecosystem functioning and their structural integration into the complex network of aboveground-belowground interactions. Briefly, the results of the three manuscripts presented here demonstrate that

- Collembola differ substantially in their direct (root feeding) and indirect effects (nutrient mobilization) on plant performance (**Chapter 3, Chapter 4**).
- Collembola may either increase or decrease plant performance, depending on the density and species composition of the Collembolan community (**Chapter 3**).
- Collembola species composition is more important for ecosystem functioning than Collembola diversity as species interactions such as competition and facilitation were shown to be prime determinants of Collembola effects on ecosystem processes (**Chapter 3**)
- Collembola effects on the functioning of grassland communities depend on plant diversity, plant functional group identity and structural complexity of the established plant community (**Chapter 3, Chapter 4)**
- Collembola and AMF interact in shaping plant competition and grassland plant community structure (**Chapter 4**).

- Effects of plant functional group identity on the belowground system are more immediate whereas effects of species and plant functional group richness take longer to materialize (**Chapter 2**).
- Grasses rather than legumes function as key plant functional group for Collembola although, from a long-term perspective, plant diversity effects are more important for soil biota than the presence of key plant functional groups (**Chapter 2**).

Taken as a whole, the present thesis highlights that **ecosystem functioning results from interactions among and within different levels of biota**. Therefore, it is indispensable not just to focus on species richness effects alone, but also consider effects of **community composition**, as well as **functional group and species identity** of plants and soil biota if we are to understand the consequences of biodiversity loss for ecosystem functioning and human well-being. Scientists will need to collaborate broadly with other disciplines in order to shed more light onto the mechanisms driving ecosystem processes and the various participants involved in the functioning of ecosystems, whether they are supposed to be keystone species or just another cog in the wheel of life.

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THE END

„Früher war mehr Lametta.“

Opa Hoppenstedt, Loriot 1923-2011